BIOLOGY AND CONTROL OF THE WESTERN PINE BEETLE

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BIOLOGY AND CONTROL OF THE
WESTERN PINE BEETLE
A SUMMARY OF FIFTY YEARS OF RESEARCH

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Many men in the state forestry organizations have contributed to western pine beetle control through the development of state laws and cooperative control projects under state assistance and guidance. Men in the state colleges have also contributed a part.* In this group Dr. W.J. Chamberlin, forest entomologist of Oregon State College, deserves special mention. For many years Chamberlin has taken an active part in different phases of forest entomology and in teaching this subject to forestry students. In 1920, he published Oregon Station Bulletin 172 on "The Western Pine Bark Beetle," which is the first and only state bulletin dealing exclusively with this pine beetle.

Many timber companies owning or operating ponderosa pine timber have had an important part in developing pine beetle control programs and in aiding research. These companies are too numerous to mention, other than a few who have played special roles. For instance, the Weyerhaeuser Timber Company has had an important part in developing western pine beetle control from the very start, and their cooperation both in research and control has been especially helpful. The Company has been active in promoting sanitation-salvage control, and has cooperated closely with the Bureau in surveys and studies of the effect of selective logging in reducing pine beetle damage. If it had not been for the active and continuous support of the Company, much of the research work on this beetle could not have been accomplished when it was.

The McCloud River Lumber Company in California deserves special mention. It has carried on beetle control work since 1912 and has actively supported cooperative research work. This Company was the first to give sanitation-salvage control a trial in California.

Other companies which have contributed materially to research studies of this beetle include the Collins Pine Lumber Company and the Fruit Growers Supply Company of California, and the J. Neils Lumber Company in Washington. Many other companies have taken an active interest in pine beetle control and have applied sanitation-salvage logging as a method of control on their operations. All of these companies have contributed to a better understanding of this bark beetle problem.

The major job of compilation was completed by the senior author in 1950 before his retirement. After his death in April 1952, the manuscript was revised, edited, and brought up to 1952 by the junior author, who assisted with the project from its start in 1941.

PREFACE

The western pine beetle (Dendroctonus brevicomis Lec.) has been the subject of more intensive study by forest entomologists and foresters during the past 50 years than any other western forest insect. This beetle has in fact been the center of a group of entomological studies - of the western pine beetle itself, of associated insects, and of certain factors that enter into the ecology and management of ponderosa pine stands. The attention which the insect has received is due to the importance of the beetle as an enemy of ponderosa pine and to its capacity to destroy timber which would otherwise be utilized by man.

The western pine beetle has been known to science since 1876, but there is every reason to assume that this beetle was a factor in the ecology of pine stands long before it was given a name. Before the era of sawmills, pine stands that approached maturity were thinned by beetle epidemics, and new trees grew up to replace those that were killed. But, as long as Indians used the forest only for hunting grounds and the first white men were interested only in trapping and livestock ranching, no one cared what happened to the trees. The beetle was not considered to be of economic importance until the advent of the lumber industry. Then as the realization developed that the supply of virgin pine stumpage was limited and that the beetle was hastening the day when the best of the old stands would be exhausted, the western pine beetle became a problem of importance to a great many people.

The beetle can upset logging programs and shorten the life of sawmill communities because it often becomes active in the woods before loggers reach the timber. The beetle takes out the very trees that the lumberman prefers to cut and mill into high-quality, soft, pine lumber. Because of this habit these beetles have sometimes been referred to as "The Pine Beetle Logging Company." The actual value of the timber that the beetles kill in any one year depends upon the current stumpage prices, and these have varied widely during different periods and in different regions. Recently the depletion of stumpage resources by beetles and the impact of this loss upon the economic life of lumbering communities and dependent industries has been taken into account in appraising the importance of the beetle problem.

One basis upon which the importance of beetle-caused losses can be fairly compared between periods and regions is the board foot volume of timber killed annually. Estimates made over the past 40 years or more have shown wide annual fluctuations. For the ponderosa pine region of the western United States, the total annual loss from the western pine beetle during this period has varied from approximately 500 million to 1,500 million board feet. The average annual loss has been estimated at about 1 billion board feet. What this loss means can best be visualized by the statement that if this lost stumpage had been manufactured into lumber, it would have supplied sawmills employing 57,000 people with an annual payroll of $18,000,000. The lumber would have produced enough material to build 100,000 5-room houses. This is a tremendous loss for western timber industries and the national lumber economy to absorb year after year.

Investigations of the biology and control of the western pine beetle began in 1900. Since 1902 continuing studies have been conducted by the Division of Forest Insect Investigations of the Bureau of Entomology (reorganized as the Bureau of Entomology and Plant Quarantine in 1934), U.S. Department of Agriculture. In December 1953, the Division was transferred to the Forest Service, Branch of Research, and became the Division of Forest Insect Research.

Many investigators in several localities of the western pine region have contributed to a steadily accumulating fund of information on the western pine beetle. Much is known about the life history and behavior of this beetle, its role in pine stands, and what can be done to control or prevent the waste of timber that it causes. But surprisingly little of this information has been published. The great bulk of the results of western pine beetle research are in manuscript reports which repose in the files of the Division of Forest Insect Research and are accessible to only a few forest entomologists. There is a definite need to extract, summarize, and publish the essential information in these reports for all who are concerned with this problem.

The present summary reviews the results of research on the western pine beetle up to 1952. It shows the progress that has been made in over a half century of study of this one bark beetle. It records the trial and errors - the research that ran into blind alleys and had to be started again with different leads, as well as the research which was successful. The summary illustrates how research progresses step by step, with many workers each contributing their bit to the building of a fund of knowledge until the final structure is completed. Starting with an insect of unknown importance some 50 years ago, research has developed a complex and intricate picture of this important bark beetle. It is now one of our best known forest insects. The research covered by this summary represents a pioneer effort in the field of forest entomology in the United States. The history of its progress and accomplishments should be of great help to research workers who are faced with similar problems. They can profit from both the failures and the successes of the work here reported.

The summary is subdivided into six sections. Section I gives an historical review of research developments from the time the insect was named in 1876 to 1952. Section II covers its biology, seasonal history, and habits. Section III discusses biotic relationships, particularly the factors which influence development of populations and their limitations by natural control factors. Section IV deals with the ecological relations of the western pine beetle and its host trees, including such important factors as host resistance and susceptibility. Section V discusses the development of western pine beetle surveys, and methods of detection, reconnaissance, appraisal, and "spotting" of trees on control projects. Section VI summarizes all of the methods of control that have been tried, and the most successful methods of dealing with western pine beetle infestations.

The more important research results are extracted or quoted from published papers and from manuscript reports. Published references are listed under Literature Cited, pages   to   , and referred to in the text by italic numbers in parentheses. Unpublished manuscripts and progress reports, which furnish the basis for most of the information summarized in this publication, are referred to by an italicized number preceded by the letter "U." A separate mimeographed list has been prepared of these reports which are in the files of the Division of Forest Insect Research, U.S. Forest Service, Washington, D.C. and in the forest experiment station files where the work originated. These files may be consulted by anyone interested in the details of the subject covered, but the reports are not available for distribution or loan. Some interpretation has been given to the results whenever this seemed desirable. Primarily the text is intended as a reference for research workers and field men who are concerned with surveys, the appraisal of western pine beetle infestations, and their control. It is believed that the summary will serve a useful purpose if it records all of the studies and experiments that have been attempted, whether the results were considered successful or not. In this way the summary can guide further study of the problem and prevent duplication and repetition of past efforts in the years to come.

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SECTION I

HISTORICAL REVIEW

Since the beginning of organized forest entomology in the western United States, the western pine beetle, Dendroctonus brevicomis Lec., has been recognized as the number one insect enemy of ponderosa pine within the region of the beetle's distribution. During the 50-year period since 1902, by far the greater part of the effort of forest entomologists in the West has been absorbed in a search for solution to the problems created by the killing of vast numbers of pine trees by this beetle and insects closely associated with it.

Figure 1 — Ghost trees left by an epidemic of western pine beetle, Modoc National Forest, California.

We can be fairly certain, however, that the first man to recognize the western pine beetle as a distinct species had no idea that this insect posed the most important entomological problem in the ponderosa pine region. This man was John L. LeConte, a surgeon in the U.S. Army during the Civil War, who was intensely interested in the taxonomy of Coleoptera. In 1850, LeConte made a trip to California, where he collected insects extensively from San Francisco to the Mexican border. Later he became Assistant Inspector of the U.S. Mint in Philadelphia and while in this position published much of his outstanding work on Coleoptera.

(Page 1a follows)

Figure 1 .- Ghost trees left by an epidemic of western pine beetle, Modoc National Forest, California.

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LeConte published the description of the western pine beetle in 1876 in the Proceedings of the American Philosophical Society. (77). He had only one specimen. How he came by it does not appear in the record. The only reference to locality is "middle California." No collector is mentioned. There is no reference to plant host. This specimen may have been sent to him by any one of several collectors who sent much material to him from the West, including G.H. Horn. Horn was also an army surgeon with the Second Cavalry, California Volunteers, from 1863-1866. During this service, Horn was stationed at Fort Tejon, Fort Crook, Surprise Valley, Sacramento Valley, and other localities in California where he may well have come into good collecting areas for the insect fauna of ponderosa pine. However, it is probable that whoever collected LeConte's specimen was interested more in taxonomy than in plant hosts or damage. Possibly this type specimen was a chance collection of an adult beetle in flight.

From 1876 to 1899, Dendroctonus brevicomis seems to have been forgotten even by the taxonomists. Dr. A.D. Hopkins in his monograph of the genus Dendroctonus (42) states: "In 1898, D. brevicomis was not represented in the U.S. National Museum. Therefore, it appears that up to 1899 there were only two specimens of the species in the large collections of the country." (The two specimens refer to LeConte's type and a specimen collected by a Dr. Dietz, labelled "Arizona," which Hopkins later described as Dendroctonus barberi).

THE PIONEER INVESTIGATIONS, 1899 - 1910

In 1899, Dr. A.D. Hopkins, then of the West Virginia Agricultural Experiment Station and considered the leading authority in the United States on forest insects, was given a special assignment under Dr. L.O. Howard, Chief of the Division of Entomology, U.S. Department of Agriculture, to make an investigation of insects injurious to forests in California, Oregon, Washington, and Idaho. As a result of a 2-months' trip, Hopkins issued his "Preliminary Report on the Insect Enemies of Forests in the Northwest" in 1899. (41). On this western trip, Hopkins was not long in collecting Dendroctonus brevicomis and in recognizing its importance. He first found it in April 1899 attacking "yellow pine" near McCloud, California, and continued to collect it in large numbers in other ponderosa pine localities. In his report (41) he states: "One species which I have provisionally identified as Dendroctonus brevicomis Lec. was found to be a most destructive enemy of the yellow pine (Pinus ponderosa) in northern California, southern and eastern Oregon, northeastern Washington, and western Idaho. A large amount of some of the finest timber in all these localities had died within the past seven or eight years, evidently as a result of attacks by this bark beetle. It was also found to attack and prevent recovery of trees injured by defoliating insects and other causes."

On this trip, Hopkins visited C.V. Piper, entomologist of the Washington Experiment Station at Pullman, Washington. Together they made a side trip into the pine forests of western Idaho to study various insects, one of these being the western pine beetle. As a result of this trip, according to Burke (15), Piper induced one of his students, J.L. Webb, to specialize in the study of forest insects. Webb, therefore, was probably the first college student of forest entomology in the United States. He collected the western pine beetle and made observations in the vicinity of Moscow and Troy, Idaho in 1900 and 1901.

From the very first, the Forest Service took an active part in encouraging the development of forest insect investigations. In 1900, the first field crew of foresters working under Gifford Pinchot discovered a bark beetle doing tremendous damage in the ponderosa pine forests of the Black Hills of South Dakota. Pinchot called upon Hopkins to investigate this situation and in 1901 and 1902 appointed J.L. Webb and H.E. Burke as Assistant Forest Experts in the Bureau of Forestry to assist Hopkins in this study. This stimulated Dr. L.O. Howard, Chief of the Division of Entomology, to start the Office of Forest Insect Investigations. This office was established in the Division of Entomology on July 1, 1902, with an appropriation of $5,800. Dr. A.D. Hopkins was put in charge. J.L. Webb and H.E. Burke, loaned from the Bureau of Forestry, were his first assistants. On July 1, 1904, these two men were transferred from the Bureau of Forestry to the newly created Bureau of Entomology. (This was later reorganized as the Bureau of Entomology and Plant Quarantine in 1934).

The first serious western pine beetle outbreak to be reported was one occurring north of Boise, Idaho, on lands of the Payette Lumber and Manufacturing Company (now the Boise Payette Lumber Company), a division of Weyerhaeuser Timber Company. Their request for an investigation was transmitted by Gifford Pinchot to L.O. Howard, Chief of the Bureau of Entomology, on August 10, 1904 and referred to Dr. Hopkins. In October of that year H.E. Burke started the first detailed investigations at Smiths Ferry, Idaho. These were followed by comprehensive investigations by J.L. Webb from May to October 1905. Webb's work served as the basis for the first Department bulletin dealing with the western pine beetle (133). Hopkins found extensive damage to yellow pine during a trip to Yosemite National Park in 1904. (103) His observations were supplemented by those of H.E. Burke at Wawona and Yosemite, California, in 1906 and 1907. Burke also made observations at Joseph, Oregon in 1907, and H.S. Barber made observations at Chester and Stirling City, California, in 1908.

All of these observations and studies culminated in 1909 when Dr. A.D. Hopkins published his comprehensive bulletins on "The Genus *Dendroctonus*" (42) and "Bark Beetles of the Genus *Dendroctonus*" (43). These publications summarized the life history, distribution, morphology, ecology, methods of control, and other information known about the western pine beetle and other *Dendroctonus*. It has been a source of continual surprise to later investigators to find how comprehensively Hopkins had covered the subject and how accurately he had deduced the beetles' habits and behavior from the meagre evidence then available.

THE EARLY SURVEYS AND CONTROL PROJECTS, 1910 - 1913

The next step was to put Hopkins' control recommendations into effect on actual control projects. This step was not long delayed, and the period of applied control soon got underway.

The first attempt to control the western pine beetle was on the Northeastern Oregon Control Project, started in 1910 when private timber owners near Baker, Oregon, became alarmed over their timber losses. The project was conducted during 1910 and 1911. The objective was largely to control the mountain pine beetle in lodgepole pine. But a considerable amount of western pine beetle infestation was also found in the ponderosa pine stands, and control of western pine beetle was a phase of the project. The Baker Forest Protective Association in cooperation with the Forest Service conducted the control work. H.E. Burke was in charge of the entomological direction of this project. W.D. Edmonston and a crew of 10 to 15 temporary men assisted with the spotting, control supervision, and checking results of the control work. Survey methods, methods of spotting trees, and methods of direct control and project organization got their start on this project.

About the same time, the District Forester of the National Forests of District 5 became concerned about bark beetle infestations in California and detailed Forest Ranger John M. Miller to conduct a survey and report upon insect conditions. The letter of instructions for this survey stated that it was "for the purpose of taking up with the Forest Officers at Supervisor's headquarters and in the field all important matters concerning forest insect infestations, and determining by work in the field the extent of such infestation and methods for its control." Miller had previously in 1909 collected the western pine beetle on the Sierra National Forest of California and had reported to the Forest Supervisor on its importance and damage. The surveys conducted by Miller during 1910 and 1911 included western pine beetle infestations on the Sequoia, Sierra, Lassen, Plumas, and Klamath National Forests.

Also in 1910, the Southern Pacific Land Company took a sudden interest in beetle control when their local agent, W.E. Glendenning, called their attention to severe pine losses on their timber holdings near Yreka, California. Through cooperative negotiations with the Forest Service, control on three projects was started under Bureau of Entomology supervision. The areas concerned were known as the Moffat Creek, Craggy Mountain, and Barkhouse projects. H.E. Burke and four assistants were transferred from Baker, Oregon to Yreka in 1911 to train spotters and give technical supervision to the control work. They also made surveys to determine results, studies of the efficiency and costs of control methods, and reconnaissance surveys in other areas to determine the need for control work. On November 16, 1911, J.M. Miller was transferred from the Forest Service to the Bureau of Entomology to assist on these projects and thus started his long career in forest insect investigations. Control work was carried on in 1912 and 1913, and surveys to determine results were continued until 1917.

During 1910 and 1911, Mr. Jackson F. Kimball, Secretary-Treasurer of the Klamath and Lake Counties Forest Fire Association, had corresponded with Dr. Hopkins regarding the significance of bark beetle infestations in the ponderosa pine stands of the Klamath Basin in southern Oregon. It was evident that the private timber owners and operators, which formed this Association and controlled a great reservoir of commercial timber, were becoming interested in the western pine beetle problem. Dr. Hopkins therefore advised setting up a field station in this locality to cooperate and in July 1911, W.D. Edmonston, with two assistants, was transferred from the Baker station to Klamath Falls, Oregon, to carry the plan into effect. The Association started one control project in the ponderosa-sugar pine type near Parker Station in 1912 under the technical supervision of the Bureau of Entomology men. The station was moved to Ashland, Oregon, in July 1912.

J.F. Kimball was probably the first representative of private timber owners to see the need for giving ponderosa pine forests the same degree of protection from pine beetles as was being given from fire. For many years he worked hard and effectively to get the pine beetle problem recognized by federal forest agencies, by the states, and by private timber owners in general. He was primarily responsible for organizing the Southern Oregon-Northern California Pine Beetle Control Project in 1921 and in getting the first large federal appropriation for cooperative control of this beetle. Through his efforts the first state pine beetle control laws were put on the books of Oregon and California in 1921, and he did much to obtain adequate financing of the basic research work. The solution of the pine beetle control problem owes much to Kimball's untiring efforts.

The McCloud River Lumber Company became concerned in 1912 over pine beetle infestations on a 46,000-acre tract near Bray in Siskiyou County, California. The Company asked the Bureau of Entomology to examine the area. The examination was made in June, September, and October 1912, under the supervision of J.M. Miller for the Bureau and Dan Stevens for the McCloud Company (37). As a result of this scouting, the Company started the Antelope Creek Control Project in 1913. This work so convinced the Company of the value of bark beetle control that they made beetle control a regular part of their operations from that time on (U44). This was probably the first time that any private timber company adopted such a plan. Much credit must be given to Elmer Hall, Logging Superintendent of the McCloud River Lumber Company for many years, who was largely responsible for developing and continuing the Company's pine beetle control program. Hall also took an active part in publicizing the need for a more aggressive program on other lands and for more adequate financing of research work. For many years, Elmer Hall was recognized as the leading advocate of pine beetle control among private timber operators in California.

In 1912, Ralph Hopping was appointed Forest Examiner by the District Forester of District 5 to continue the bark beetle survey and control work started by J.M. Miller. During his period of service as a Forest Ranger, Hopping had been interested in insect taxonomy and had made extensive collections in the field. One of the first projects coming under Hopping's supervision was the Hayfork Valley Project on the Trinity National Forest. This infestation had first been reported by Forest Guard Oscar M. Evans in December 1911. It was later examined more thoroughly by Deputy Forest Supervisor J.D. Coffman and J.M. Miller for the Bureau of Entomology in late February 1912. Control work started November 12, 1912 and continued until January 7, 1913. Other projects supervised by Hopping in 1913 included the Seiad Project on the Klamath, the Goodyear Project on the California, and the Contour Project on the Sierra National Forest.

Hopping continued to carry on surveys and control of the western pine beetle on these and other national forests of District 5 until 1920, when he resigned to do similar work for the Canadian government in British Columbia. In 1916 he prepared a mimeographed paper, "Manual of Insect Control for California," which was the first American manual of bark beetle control. (148A).

It was on the Klamath projects in 1913 that Hopping took issue with Hopkins, who had insisted that his "percentage principle of control" be applied. In the percentage principle of control only 75 percent of the infestation is treated. Hopping believed that as nearly 100 percent as possible of the infestation should be treated. The dispute was finally resolved by Chief Forester Henry S. Graves in Hopkins' favor (15) and the control results, which appeared to be excellent, vindicated Hopkins' position. (On later projects 100 percent treatment was usually striven for, but rarely attained).

In 1912, J.F. Pernot, a graduate forester and entomologist of Oregon State College, was assigned to the District Office of the Forest Service at Portland, Oregon, to study forest insect outbreaks in Oregon and Washington and supervise control projects. During the period 1912 - 1914, the mountain pine beetle infestations in lodgepole were active on tremendous areas in eastern Oregon, and in many cases western pine beetle infestations were also present. Pernot devoted most of his time to surveys and control of these outbreaks, including projects on the Ochoco and Whitman National Forests. Pernot was killed in a horseback accident on the Ochoco in 1914.

Control work was also started in Yosemite National Park in 1913 under the direction of J.M. Miller. This was the first forest insect control conducted in any of the national parks. Control has been continued on an annual maintenance basis ever since. (103) / Other national parks which have bonducted control of the western pine beetle include Sequoia-Kings Canyon, Lassen Volcanic, and Crater Lake National Parks.

These early years of applied direct control of western pine beetle outbreaks developed many of the control techniques, such as the fell-peel-burn method, developed methods of surveys and spotting trees for the control work, and developed project organization. The results in controlling the beetle were sometimes satisfactory but in too many cases were not.

BIOLOGICAL AND EXPERIMENTAL CONTROL STUDIES, 1914 - 1924

The early control projects showed that there was still much to be learned about the biology, habits, epidemiology, host relations, and methods of controlling the western pine beetle. So detailed investigations were renewed at the Ashland, Oregon, station under J.M. Miller's direction in 1914. In August of that year, F.P. Keen and J.E. Patterson joined the station staff. Keen carried out detailed biological and quantitative studies of this beetle on the Lamb's Mine unit of some 2,500 acres south of Ashland. Many population studies based on brood counts were made during this period. Patterson started attraction and solar heat studies. The station staff also made annual estimates of the quantity of infestation on each of several units of pine type on the mountains bordering the Rogue River Valley. These surveys were continued for 10 years.

At Coeur d'Alene, Idaho, J.C. Evenden made life history studies of the western pine beetle in Kootenai County, Idaho, in connection with phenological studies in that area.

In 1916, A.J. Jaenicke was transferred from the Southwestern District of the Forest Service to the office of District 6 at Portland, Oregon, to take the position made vacant by Pernot's death. As Forest Examiner his assignment was to conduct insect surveys and supervise control in the national forests of Oregon and Washington. He worked closely with the Bureau of Entomology in making preliminary surveys, in handling the technical supervision of control work, and in inspecting results. During his long period of service, still continuing in 1952, he had a part in organizing or supervising all of the bark beetle control projects in Oregon and Washington. He made many contributions to the advancement of knowledge of the western pine beetle.

The San Joaquin Experimental Control Projects, 1920 - 1924

The results of research on biology and habits of the western pine beetle at the Ashland station, and the unsatisfactory results on a number of the early control projects, led to the development of new ideas which offered some promise of application in control practices. The Forest Service became interested and an agreement was reached with the Bureau of Entomology to test several of the proposed theories on experimental control projects. This program was outlined in what became known as the Ashland Conference Plan of June 1917. The plan called for a series of experiments in the San Joaquin River drainage of the Sierra National Forest in California. Tests were proposed of the percentage principle of control as advocated by Dr. Hopkins, the effectiveness of continued or "maintenance control" to prevent epidemics, and the costs and efficiency of summer control by means of solar heat. (U96)

A field station was provided at the forest supervisor's headquarters at North Fork, California, to carry out the Bureau's part of this project. J.M. Miller was in charge with from one to three assistants. The control work started in 1920 and was continued until 1924. The results of this experimental work are fully discussed later in this paper.

THE PERIOD OF MAJOR DIRECT CONTROL PROJECTS, 1920 - 1936

As a result of conferences between the Forest Service and the Bureau of Entomology, an agreement was reached in 1920 whereby the Forest Service delegated its responsibilities for surveys and the supervision of control projects to the Bureau. The Bureau continued to conduct research work and advise other agencies on control. This agreement was made official by the Secretary in a memorandum entitled: "Principles of Cooperation between the Forest Service and the Bureau of Entomology in Insect Control in the National Forests." It became effective February 16, 1920. The technical men of the Bureau thus became responsible not only for the research work in developing forest insect control measures, but for putting their results into practice on the national forests. The Forest Service continued to designate some officer in the Division of Timber Management as in charge of insect control work, to supervise the administration of control projects, and to act as a lidson officer between the two bureaus. Under this arrangement there was very close cooperation between the two services, and the agreement continued through 1953, when forest entomology activities were transferred to the Forest Service.

The Southern Oregon - Northern California Pine Beetle Control Project, 1921 - 1924

Increasing infestations of western pine beetle in the Klamath Basin of southern Oregon and northern California from 1918 to 1920 impressed private timber owners with the need for action. Pressure was put upon the U.S. Department of Agriculture for a renewal of the survey and control program which had been allowed to lapse after the first station closed in 1912. Jackson F. Kimball, Secretary-Treasurer of the Klamath Forest Protective Association (previously the Klamath and Lake Counties Forest Fire Association), an organization which included all of the private holders of ponderosa pine timber in that section, called a meeting in April 1921 at Klamath Falls which was attended by representatives of the leading pine owners throughout the Western States and by state and federal forestry officials. An aggressive control program was endorsed by this group. As a result of this meeting, action was started to obtain federal appropriations to enable the Forest Service and Indian Service to conduct control work on their own lands and to cooperate with the private owners in a comprehensive control operation embracing 1,267,000 acres of ponderosa pine forests.

In September 1921, A.J. Jaenicke was assigned to Klamath Falls to work on this project. The first step was to run surveys to determine the extent to which the infestation involved the multiple ownerships of the Klamath Basin. In this survey program, Jaenicke was assisted by F.P. Keen from the North Fork station, J.E. Patterson of the Ashland station, and J.C. Evenden of the Coeur d'Alene station.

As a result of the information that was obtained and the recommendations that were made, a special appropriation of $150,000 was obtained for control work on federal lands and for the necessary technical services by the Bureau of Entomology. The Klamath Forest Protective Association assumed the obligation for financing the work on private lands. This program, which extended over a period of 3 years, was called the Southern Oregon-Northern California Pine Beetle Control Project.

A field station to carry out the functions of the Bureau of Entomology was established with project funds early in 1922 with F.P. Keen in charge. General administration, coordination of work, and fiscal control of the project was handled under a Board of Control consisting of a representative of the Forest Service, Indian Service, private owners, and Bureau of Entomology. Keen as Bureau representative was elected chairman of the Board. Keen recruited a staff of men and trained them as spotters and in the details of survey and control methods.

The project started in the spring of 1922 (59) and continued through the fall of 1924, when all of the epidemic units had been treated. During this period, 31,512 trees containing 35,005,620 board feet of lumber were treated on 393,507 acres at a total cost of $144,880. This control work was credited with saving 46,739,000 board feet of timber.

This project was the stimulus for a number of research projects. Studies were started by Person on the effectiveness of predators and how they might be saved in the control work (106), and studies of the long time trend of beetle epidemics as shown by yearly cruises of sample plots were started by Keen. (see p.297)

This project showed that direct control of western pine beetle was a very costly undertaking and, while effective in reducing losses for temporary periods on the areas treated, did not provide a fully satisfactory answer to the protection of vast tracts of infested commercial pine timber. Some cheaper, more effective, and lasting means of protection was needed. The project closed in November 1924. By that time the original appropriation was exhausted and the private timber owners decided to continue control work more independently. A limited amount of control work on some of the more accessible and valuable areas was continued by them and by both the Forest Service and Indian Service for a number of years, but never on a large enough scale to cope with the tremendous problem. (79).

The Berkeley and Portland Forest Insect Laboratories, 1930 - 1952

Expanding research, surveys, and control activities in the western pine beetle field called for a reorganization of the Bureau of Entomology's field laboratories in 1930. In September of that year, the California laboratory, with J.M. Miller in charge, was moved from Stanford to the University of California campus at Berkeley, where quarters were provided by the School of Forestry. This move established close contact of the research work with the Forest Experiment Station of the Forest Service, and with the School of Forestry and Division of Entomology of the College of Agriculture. At the same time a new laboratory was established in cooperation with the Pacific Northwest Forest Experiment Station at Portland, Oregon, to serve the territory of Oregon and Washington. F.P. Keen was selected to take charge of this new laboratory. For the next two decades, a great amount of research on the western pine beetle, surveys, and the supervision of large control projects was centered at the Berkeley and Portland Laboratories and their outlying field locations.

The CCC Program, 1933 - 1942

Inauguration of the Civilian Conservation Corps program in 1933 provided an opportunity for direct control on a scale more commensurate with the size of the problem. Control work was greatly expanded on federal lands suffering from beetle damage. In California, Oregon, Washington, and Idaho a number of CCC camps devoted part or all of their activity to this "bug" work. In Oregon and Washington some 98,000 infested ponderosa pines were cut and treated by CCC labor at a cost estimated at $555,510. By far the larger amount of this work was conducted on the Klamath, Warm Springs, and Yakima Indian Reservations. This work was largely under the supervision of Harold Weaver, who gave it careful attention, and analyzed the results in a series of comprehensive reports. (U307,U308,U309).

Although this control work was not considered experimental in character, it did contribute to knowledge of the effectiveness of direct control and of the difficulties and limitations of a program of this kind. Much of research value came from this control effort, including surveys which charted the rise and fall of epidemics, studies of the effect of freezing weather on beetle populations, and records of the effectiveness of control work in reducing and maintaining a low level of timber losses.

The liquidation of the CCC program and the beginning of World War II brought to a close the era of large scale projects for the direct control of the western pine beetle. The large investment in manpower needed to cover extensive forest areas, the heavy costs, and the generally mediocre and temporary results discouraged further use of direct methods on commercial forest areas. Only on some intensively used park and recreational areas, where high timber values justified a greater investment in control, was maintenance control continued.

Figure 2 --Nearly complete destruction of a ponderosa pine stand by the western pine beetle, Modoc National Forest, California.

THE FOREST MANAGEMENT APPROACH SINCE 1924

Until 1924, the principal emphasis had been upon the biology of the western pine beetle and its control through direct measures. In July 1923, F.C. Craighead succeeded A.D. Hopkins as Chief of the Division of Forest Insect Investigations. Soon after Dr. Craighead took over direction of the work, he suggested that the western pine beetle might, in fact, be secondary to tree condition brought on by drought and other weakening effects. Through his encouragement a new line of investigations was stimulated. A series of new studies was started dealing primarily with the host tree, its growth as affected by climate, its resistance or susceptibility to attack, and its influence on the progress of epidemics. (25). Behind these studies was always the thought that if enough were known about the beetle's relation to the host tree, it might be possible to control outbreaks through forest management practices.

(Page 22a follows)

Figure 2.- Western pine beetle killed snags, representing nearly 50 percent of the original stand, are all that is left following logging, Modoc County, California.

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A study of the effect of climate on tree growth was started in 1924 (U87) and continued for several years (68). Tree resistance and susceptibility studies were started by Person and Keen which led to tree classification and the development of sanitation-salvage logging.

It was fortunate that about 1937, when the CCC program of direct beetle control was on the decline, results from sanitation-salvage logging at Black's Mountain Experimental Forest in California showed great promise. The results in beetle control by this selective logging method were so encouraging that the emphasis quickly shifted from direct to indirect control in commercial forests. Not only was reduction of losses greater and more lasting than with direct control, but the profits from the timber cut more than paid for the extra cost of this type of logging. Private timber companies and federal forest agencies adopted this method wherever feasible. Direct control was practically abandoned except for special situations in parks and recreational areas, or where outbreaks appeared to be developing rapidly in areas which could not be readily reached in logging. It appeared to many foresters and timber owners that the solution of the western pine beetle problem had finally been found.

STUDIES WITH NEW INSECTICIDES, 1944 - 1952

With the development of DDT and other synthetic organic insecticides during and after World War II, a new period of research on direct control of the western pine beetle got underway. There was hope that some one of these extremely potent new insecticides might be used more effectively in control than any of the older methods. There was also the possibility that through residual action a spray containing one of these new chemicals might be used to protect especially valuable trees, such as those on recreational areas or around summer homes.

DDT in oil was first tried to prevent attack by the western pine beetle on trap trees and logs by R.C. Hall in 1944. Other new insecticides were tested, as penetrating oil sprays and residual sprays, by J.E. Patterson, A.D. Moore, L.W. Orr, and other investigators from 1945 to 1952. Of the various chemicals tested, ethylene dibromide proved most effective in killing beetles when applied as a penetrating oil spray. It was used on several control projects where sanitation-salvage logging was not appropriate, such as on inaccessible forest lands or on parks and recreational areas. But killing beetles with chemicals was subject to the same disadvantages of costs and short-time effectiveness as killing beetles with fire or other of the older direct control measures. It was a palliative but not a cure since it did not change the basic susceptibility of the timber stand.

The possibilities of preventing attacks through protective sprays had been investigated but not fully explored by 1952.

After the retirement of Dr. F.C. Craighead, Dr. J.A. Beal was appointed Chief of the Division of Forest Insect Investigations in August 1950. The short period from 1950 to 1952, when this account closes, was characterized by improvements in chemical control techniques, standardization of sanitation-salvage control practices, and review and summarization of results of the first 50 years of western pine beetle research.

The completion of this review does not mean that we can write "finis" to investigations of the western pine beetle. Many phases of the research have been merely exploratory, and the answers not yet found. More detailed research is needed on flight habits, on attraction and resistance of host trees, on resistant strains of pine, on the underlying causes of epidemics, and on methods of predicting epidemics. These are only a few of the more obvious unsolved problems, which should give future research workers plenty of room for expanding knowledge of this important forest insect.

SECTION II

BIOLOGY, SEASONAL HISTORY, AND HABITS

GENERAL

Taxonomy

The original description of Dendroctonus brevicomis published by LeConte (1876, p.386) was of a single specimen from middle California. While this first description has been somewhat modified by other taxonomists from study of larger series of specimens, the validity of the species has apparently never been questioned. Hopkins in his monograph of the genus Dendroctonus (42) states that LeConte's type was a male and that the description agrees with the specimen "except that the prothorax is not nearly twice as broad as long." He gives a full technical description of typical females and males.

Swaine (124) gives the following brief technical description of the adults:

> "Length, 3.2 mm. to 5 mm., average 4.2 mm.; colour dark brown to black; the front elevated on each side of a deep median groove in the male, faintly so in the female; sides of the epistomal process oblique; the pronotum shining, hardly constricted in front, feebly so in the male; the elytra as wide as the pronotum; the striae faintly impressed, the strial punctures very small, the discal interspaces densely, finely asperate, the declivital striae faint; broadly impressed on each side of the elevated suture; the pubescence rather abundant, everywhere short, erect, and inconspicuous, with a few slightly longer hairs intermixed on the declivity. The female has a narrow, transverse elevation across the pronotum behind the cephalic margin, continued across the sides; the male has a transverse depression similarly situated."

Hopkins (43) gives the following brief general description of the beetle:

> "The western pine beetle is a rather stout, brownish, cylindrical bark beetle from 3 mm. to 5 mm. in length, with broad head and grooved pronotum punctured and but slightly narrowed toward the head and elytra with fine rugosities, but entirely without hairs."

Very closely allied to D. brevicomis is the southwestern pine beetle, D. barberi, which attacks ponderosa pine in Arizona and New Mexico, but does not overlap the distribution of D. brevicomis. For the layman these two species are difficult to distinguish, but according to Hopkins D. barberi can be distinguished from D. brevicomis by "the prevailing coarser rugosities of the elytral interspaces and the distinctly impressed striae." Swaine (124) confirms this character for the separation of the two species.

For practical purposes of identification in the field, the egg galleries cut by beetles in the inner bark provide a simple and reliable character for distinguishing the work of the western pine beetle from that of other scolytids within its range. These egg galleries, which will be described later, form a winding, criss-cross pattern unlike that of any other species of bark beetle with which it is associated. The egg galleries of D. barberi are very similar except that, according to Hopkins, they are "usually distinctly transversely winding," instead of "subtransversely winding."

Host Trees

It is well established that the western pine beetle is highly specific in its host selection. Four tree species appear in the host records, but two of these can be considered as accidental.

Pinus ponderosa

This tree species was first listed as a preferred host by Hopkins (42,43) and all subsequent publications agree in placing ponderosa pine first as the selected host of the beetle. The high value of ponderosa pine for lumber production is largely responsible for the importance that has been attached to the western pine beetle problem.

Pinus coulteri

Unpublished notes in the files of the Forest Insect Laboratory at Berkeley reveal that the beetle was first collected from Coulter pine in 1915 near Julian, California, by F.P. Keen. Specimens sent to Dr. A.D. Hopkins at that time were tentatively identified as *Dendroctonus barberi*. Later Hopkins made a careful study of the material and changed the determination to *D. brevicomis*. It is now generally conceded that the range of *D. barberi* is limited to the southwestern pine region of Arizona and New Mexico and that this species does not occur in California. Throughout southern California the western pine beetle has been found to attack Coulter pine in equal preference to ponderosa pine.

Pinus lambertiana

Hopkins (4243) records the occurrence of the western pine beetle in sugar pine, but this record was questioned soon after the first detailed investigations were started in the West. Hopkins' original notes indicate that the beetle was found in what was considered to be a sugar pine log at a mill near Grants Pass, Oregon, but there was some uncertainty as to the tree species from which the log came. Continued observations by other workers on field surveys extending over many years have failed to record a single authentic case of attack on sugar pine under normal forest conditions. According to Miller (U169) experiments to force attack by the beetle on sugar pine logs in cages resulted in the beetles entering the bark and extending short egg galleries, but no broods developed successfully.

Pinus contorta

Records of attack on lodgepole pine under natural conditions near Bly, Oregon, were reported by Keen (62,63). This occurred where lodgepole was growing in proximity to heavy grouping attack by the beetle on ponderosa pine and seems to have been due to an overflow of population around centers to which the beetles had been attracted. In one case there was evidence of successful brood development in lodgepole. Chamberlin (19) also mentions lodgepole pine as an accidentalhost of the western pine beetle in addition to sugar pine.

Distribution

Hopkins (42,43) lists localities in California, Oregon, Washington, and Idaho where the beetle was collected before 1909. Keen (74 p132) states: "The western pine beetle is the most important insect enemy of ponderosa and Coulter pines within the range of these trees from Baja California north into Oregon, Washington, Idaho, Montana, and western Canada." The species has not been collected in Baja California, nor east of the Continental Divide in Montana. It is associated with the Pacific Coast form of Pinus ponderosa and is not found in Pinus ponderosa var. scopulorum through the Rocky Mountain range of this variety. (Figure 3)

Figure 3 .-- Distribution of the western pine beetle (Dendroctonus brevicomis Lec.)in the western portion of North America.

(Page 30a follows)

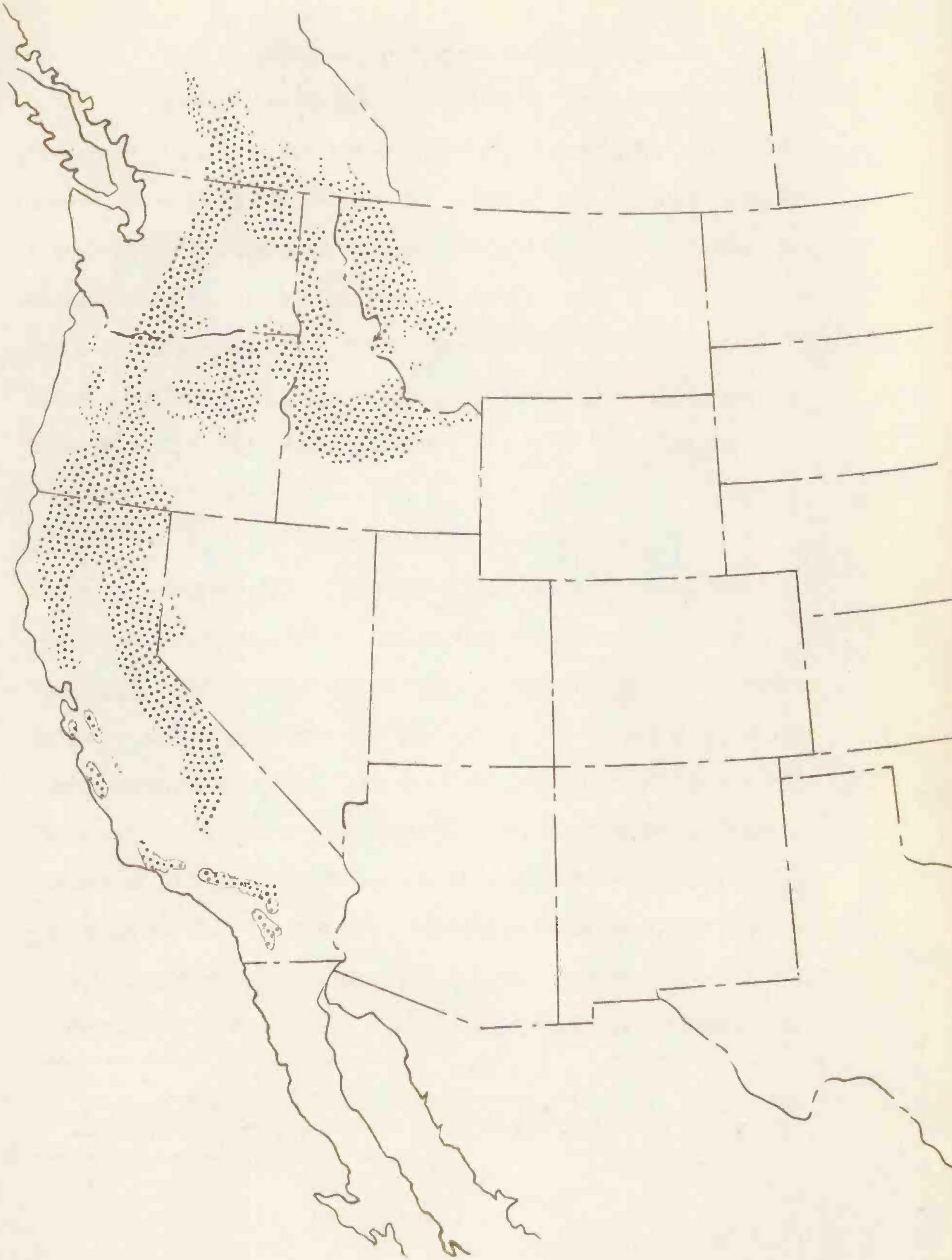

Figure 3.-- Distribution of the western pine beetle (*Dendroctonus brevicomis* Lec. in the western portion of North America.

THE ADULT BEETLE

The life history of a western pine beetle can be considered to begin with the egg, which is deposited by the parent beetle alongside the egg gallery in the inner bark of a pine tree. The larva, which emerges from the egg feeds for a time by boring a tiny mine in the inner bark, then turns outward and enters the outer bark where it completes its feeding and matures. The final activity of the larval stage is to enlarge its mine in the outer bark into a cell in which pupation and the transformation to the adult stage take place. During all this period of feeding, growth, and development, there are many hazards and the mortality is high among the larval broods.

Finally, however, those larvae that succeed in completing their development and survive the transformation as pupae reach the adult stage. From this point on the adult passes through a series of activities that make up the life of a beetle - emergence from the tree in which it has been reared, a period of flight, attack upon another tree, mating, egg gallery construction, oviposition, re-emergence, and possibly attack upon another tree - until the beetle finally dies. Usually death comes at the end of one of its egg galleries unless it meets with some accidental circumstance that brings it to an untimely end.

For the purposes of this summary it is necessary to select some one point in the life cycle where we can begin to assemble the accumulated information on life history and review the studies that have been made, and then continue on with each succeeding stage until the circle has been completed. It would seem logical to begin with the egg stage, but this is complicated by the fact that the egg first begins in the body of the parent beetle and the place where it starts incubation is determined by the activities of the adult just prior to oviposition; consequently, it seems best to start summarization with the attack upon the tree and the activity of the parent beetles just before this event.

Figure 4 .—The four stages of western pine beetle: A, Eggs; B, Larva; C, Pupa; D, Adult. Each 8 times natural size.

Size and Color of Matured Adults

Individual beetles, even after becoming fully mature, vary appreciably in size and color. LeConte described the type male as "red-brown." Hopkins stated the color variously as "light brown" or as "brownish to nearly black." Swaine says they are "dark brown to black." Adults are light brown if not fully mature, but gradually darken to brown or nearly black.

The relative size of the beetle has been given some special attention because it was believed that this was an indication of adequate nutrition during the development of the brood. Hopkins gives the length as 3 mm. to 5 mm. In 1941 Yuill (U336) compared the size of adults emerging from high risk trees with those from low risk trees using weight as an index. On the basis of 2,790 newly emerged adults, he found that those from high risk trees average 6.2 mgs. per beetle, while those from low risk trees averaged 4.0 mgs.

(Page 32a follows)

A

B

C

D

Figure 4 .- The four stages of western pine beetle:
A, Eggs; B,larva; C, pupa; D, adult. Each 8 times natural size.

A - PS635
B PS 868
C PS 870A
D PS 872A

Further measurements of length were made by Hall and Startt on the Hat Creek area during the 1942 season and recorded only in field notes. They found a range in beetle size from 3.1 mm. to 5.2 mm.; 500 males averaged 4.15 mm., while a similar number of females averaged 4.38 mm.

Ratio of the Sexes

The few studies that have been made on this point indicate that there is an unequal distribution of males and females. In the first Ashland studies, Keen (U126) made sex determinations from some 428 emerging adults and also from the adults collected from 66 new attacks. It was found that "Females, both in emerging and attacking, outnumber the males by a ratio of 54 to 46. Polygamy is found to occur."

Life Duration of the Adult

The question of how long the adults may live, both before and after they make their attack on a tree, has been given little study except in the first biological investigations which were made at Ashland, Oregon, in 1916. From a summary of records on parent adults in 14 trees attacked in the fall of 1915 and from which the new broods emerged in the spring of 1916, Keen (U126) found that "the average life of parent adults overwintering in the tree /is/ ...214 days or about 244 days total life (including an estimate of 30 days from the time beetles first form until trees are attacked). The maximum (life) is a total of 270 days." When deprived of their normal food supply by being kept in a glass tube with a cotton stopper, both parent adults and new adults "died within about 15 days."

The parent adults recorded by Keen were obviously in a winter brood tree and went through the colder winter months in a dormant condition. This period of arrested metabolism undoubtedly extended the duration of life much longer than if the beetles had been continuously active as in summer generation trees where activity of parent adults is continuous throughout their life span.

Food Habits

It can be assumed that in order to live as long as these observations indicate, the adult beetles must feed, and the fact that they die rather quickly if confined where no food is available is further proof of this point. Keen (U126) inquired into the matter of food habits and concluded that: "It was not definitely determined whether the adults feed while constructing their galleries,but they probably do. The major portion of the frass in the galleries is made up of small pieces of wood cut out of the gallery and placed to one side." It was not until 1929 that the food requirements of the adult became a subject of detailed investigations. These studies were stimulated by the possibility of finding atrahents which could be used in trapping beetles as a control method; this led to a search for the materials in ponderosa pine that make certain trees especially attractive to beetles.

Struble (U284) carried out a study of the material found in the alimentary tract of the beetle and conducted a series of experiments to determine the periods of its activity when the beetle feeds and what parts of the tree are used as food. It was thought that the adults might feed on pine foliage or other plants during the flight period as is the case with some other beetles that breed in cambium. For instance, the adults of a related genus of *Phloeosinus* spp. feed in twigs of their cedar host plants before they attack the main bole and oviposit. Another case is that of the pine flatheaded borer, *Melanophila californica* Van Dyke, which is known to feed on pine foliage before it oviposits on the tree. In these studies, Struble found that the western pine beetle ingested outer bark into the alimentary tract before it emerged, and inner bark while constructing egg galleries. He also found a yeast present in the digestive tract of the beetle which actively inoculates the inner bark tissues when the beetle enters a living tree. Struble's conclusions were:

> "1. The beetles feed continuously during the time they are in the bark (outer) prior to exit and while they are extending their egg galleries.
>
> 2. Adults do not feed on needles or twigs of yellow pine.
>
> 3. A yeast is definitely associated in the digestive tract."

In 1930 Jeffrey (U103) followed up these nutritional studies, giving particular attention to the biochemistry of bark and phloem materials ingested by the adults. He summarized the feeding habits of the adults as follows:

" Period	Material Ingested
First day or two (after pupal stage)	none
During emergence	outer bark
During flight	none
While entering tree	outer bark
While constructing galleries	inner bark "

Jeffrey's further investigations turned to an analysis of the phloem materials to see if trees selected by the beetles for attack showed any significant differences from trees that were not attacked. While considerable attention was given to the availability of food materials for the larval broods, no further observations were made on feeding habits of the adults. However, his chemical analyses of the inner and outer bark indicate that these contained sufficient sugars and starches in available form to provide nutrition for the adults.

The Attack

Description

The method of attacking a tree is one phase of the beetle's activity that can be closely observed and it has been described in several reports. In describing the attack, Webb (133) states:

> "Large numbers of the beetles usually settle upon a few trees close together and crawl about upon the bark from near the base to about two-thirds of the distance to the tree top seeking suitable places for entrance. Crevices in the bark are favorite places with them for this purpose."

After observing the attack on a series of trees on the Lamb's Mine Unit in 1915-16, Keen (U126) recorded the following:

> "A female was observed to alight on a log and after 5 minutes of walking around and examining it, started boring into a crevice within 6 inches of where she lit.
>
> There appears to be no sudden or concerted attack on the part of the beetles, but rather a slow continuous attack depending upon the abundance of the beetles striking the tree at some weak point near the top and then gradually extending the attack down the trunk until resistance of the tree is gradually overcome."

Person (U229) gives a description of the initial phases of an attack which he followed on a tree in the Cascadel Unit in 1926.

> "Flight to the tree started shortly after sunrise and continued until about sunset. The flight is spasmodic. A number of *D.b.* would fly to the tree and when they becamequite abundant, a number of *Enoclerus lecontei* (*Thanasimus nigriventris*) would appear both by flight and by crawling from other parts of the tree. This would cause the *D.b.* to hide in bark crevices and under the bark scales or drop to the ground. Then in a short while the *T. nigriventris* would disperse and another group of *D.b.* would fly to the tree. This would continue throughout the day during the entire period of flight to this tree if weather conditions were favorable. Between 8:30 A.M. and 9 A.M. on May 14, a total of 14 *D.b.* flew to this tree and lit inside of a bark area of about 6 square feet. This is about as heavy a flight as was observed during the season. Some of the beetles held onto the bark where they lit while others fell to the ground."

Character of Bark Selected for Attack

As the beetles attack a tree to which they have been attracted, they invariably make a selection of the bark area which they enter. The attacks are made only in bark areas that have formed the corky layers of the outer bark; the young thin bark on ? the upper bole and limbs is usually avoided. Consequently the attack near the top of the main bole does not extend above the corky bark so that usually a diameter of from 4 to 8 inches marks the upper limit of infestation. The limbs of large pines are rarely attacked and then only when their bark surface has aged to the point of forming cork plates. Young trees up to 6 to 8 inches in basal diameter are fairly immune to attacks by the western pine beetle.

One explanation for this selective habit may be found in the fact that as the larvae develop they complete their feeding and transformation in the corky layers of the outer bark. The adult, therefore, in selecting the place for oviposition avoids the younger trees and those parts of the older trees which do not provide this outer bark medium for the later states of brood development.

Location of First Attacks

Usually the first attacks are made in the top of the tree or upper bole and then progress up and down to include all of the corky bark area. The basal portion of the tree, which retains moisture in the bark and sapwood the longest, is the last to be attacked, or may be ignored entirely.

Density of Attack

Beetles seem instinctively to distribute their attacks over the bark surface so that excessive overcrowding does not occur in any particular bark area. After a certain number of beetles have started their attacks within a square foot, the later arrivals seek entrance elsewhere in bark surfaces not already occupied. This habit is necessary in order to prevent overcrowding of the available food supply for the larval broods. While many pairs of beetles could easily attack the same square foot of bark and construct egg galleries, the larval broods developing under such conditions would exhaust their food supply before they became full grown and thus be doomed to starvation. Consequently we find that the beetles seldom carry the density of attack to the point of overstocking the bark except under exceptional conditions. Although considerable variation in the number of attacks per square foot of bark is the rule, this density has been found to keep always within certain limits.

Keen (U126) on the Ashland areas found that "the attacks per square foot of bark ranged from 2.5 to 11 and averaged 6.8."

Person (U229) in the Cascadel studies found a difference in density of attack between the first generation trees attacked in the spring and early summer and the second generation trees attacked after the seasonal growth period had subsided. He reported:

"Generation	No. square feet counted	Average attack per square foot
1st 1926	193	14.3
2d 1926	184	10.

> "The greater number of attacks on the first generation trees may have been due to the ability of the trees to offer more resistance in the spring than in the summer; and also the fact that there was a greater number of beetles in the first generation than in the second generation flight."

Where large populations have built up and the beetles are forced to attack trees of more vigorous growth rate, the density of attack has been found to increase. Miller (86) reported that 20.6 beetles per square foot attacked standing trees after emerging from windfalls on the California National Forest in 1921. "The attacks within the bark were so numerous that there was not enough food to supply all the developing broods; as a result the emergence following these attacks was only half of normal."

Patterson (U209) and Miller (U187) recorded the attacks per square foot from over 2300 square feet of infested bark collected in southern Oregon and the central Sierra Nevada areas. Finally in 1928 Keen (U138) summarized and analyzed statistically all of the beetle population statistics which had been accumulated by different observers up to that time. From a total of some 4,177 square feet of infested bark examined, he found that the different averages which had been arrived at ranged from 5.5 to 21.6 attacks per square foot, but that the general average for all of this material was 11.6 attacks per square foot.

Figure 5 .--Paper tags show density of western pine beetle attack on lower bole of ponderosa pine.

Duration of the Attack

When a tree is successfully attacked, the beetles keep coming until they have overcome its resistance and occupied most of the selected bark surface. The length of this period is quite variable. Keen (U126) describes an attack which extended from April 25 to July 3 on the same tree, beginning at the top and extending gradually to the base. In another tree the attack extended from March 11 to May 4. This type of attack was found to be typical of a great number of trees on the Lamb's Mine Unit in 1915. However, Keen states that "during the height of the attacking period, some trees were attacked so rapidly that it is as though they were attacked simultaneously throughout their length."

(Page 42a follows)

Figure .5- Paper tags show density of western pine beetle attack on lower bole of ponderosa pine.

BEPQ #6011

Person (U229) records the period from the first attack to the time when the tree was overcome for four trees on the Cascadel unit in 1926. The attack on the base of these trees was forced by caging, but the main force of the attack came to the trees above the cages from beetles flying in the area. One of these trees required from April 29 to May 20, a period of 21 days, before it was overcome; the other trees were killed in 7, 9,and 9 days respectively.

It can be concluded on the basis of the evidence that the period of attack varies with the supply of beetles flying in the area. Under epidemic conditions attacks occur in great force and most of the trees are killed within a period of a week to 10 days. When the beetle population is light, attacks may be greatly prolonged.

Another factor that may prolong the period of attack is the resistance of vigorous trees. Person (U229) states: "The period between first attack and the date on which the tree was overcome was over twice as long for the fast growing tree."

Group Attacks

The first beetles starting an attack are nearly always attracted to some particular tree. If this is overcome and other beetles still keep coming to this same center of attraction, they do not attempt to occupy all of the bark of the initial tree but begin an attack on an adjacent tree. When the bark of this second tree is occupied, another tree nearby will be attacked, so that if the beetles keep coming a group of attacked trees builds up around the initial center of attraction. Under highly epidemic conditions, a group may include as many as 200 trees, but ordinarily from 3 to 15 trees will absorb the force of attacking beetles drawn to any one center. A "key" tree, the one selected for the initial attack, can be found in almost all groups. Endemic conditions are marked by the attacks being limited mostly to single trees.

Sex Making the Initial Attack

Webb (133), Keen (U126), and Person (U229) all made observations which showed definitely that the female starts the attack. She finds a suitable spot in a crevice of bark and bores almost directly into the phloem. About the time she reaches the phloem she is joined ? jointed by the male who assists by pushing the excavated frass out of the entrance hole. The female continues the gallery and is followed by the male who has never been observed doing any of the actual excavating work but does help by working the pitch away from the entrance. Callaham (X) has observed that the male does not even appear until the pitch starts to flow.

no refere

Mating Habits

According to Keen (U126) females in flight and those found just entering the tree cannot produce fertile eggs in trap logs from which the males are excluded. Only after the female has been joined by a male in the entrance chamber do the eggs become fertile. From this Keen concluded that copulation takes place in trees and not during the flight period. There are no records of copulation having been actually observed, which still further supports the theory that fertilization takes place after the beetles enter the bark.

Number of Beetles Per Attack

Keen (U126) found some evidence of what he considered to represent polygamous relation: On 20 square feet of bark of one newly attacked tree, 66 attacks were noted with a total of 171 parent adults or 2.6 beetles per attack. Of these, "11 attacks were found containing 3 beetles each, of which 2 were females and 1 was a male." This showed the same percentage division between the sexes as subsequently emerged from this tree, namely 54% female and 46% male. "In these polygamous galleries, sometimes the two females were found in the lead, one at the extreme end doing the construction work, the second female about one inch behind, and the male two or more inches in the rear of the last female. In other cases the male was found in the middle of the gallery with one female in the lead and one behind him nearer the entrance."

Hopkins, commenting by letter on this evidence, questioned whether it signified polygamous habits: "The presence of an additional female may have been purely accidental and not permanent, or she may have been fertilized by another male in an adjacent or connecting gallery. Further observations are necessary, but it is not an important question to settle anyway."

Person (U229) from an examination of 29 square feet of bark on the North Fork, California, area reports finding an average of 12 attacks per square foot, but only two beetles with each attack.

Patterson (U209 reported 304 adults in 133 attacks that were counted by P.D. Sergent in the Ashland, Oregon, area. The number of beetles recorded per attack ranged from 1 to 5 with an average of 2.3.

Pitch Tubes

Formulation of the "pitch tubes" which appear on the outer surface of the bark soon after the attack starts is described by Webb (133).

> "As the first incision is made into the living inner bark, the tree begins exuding pitch to cover the wound made by the intruding beetle. This pitch or resin collects at the mouth of the entrance hole in the form usually known as a pitch tube. Where the attacking force of beetles is small, the efforts of the tree to heal these wounds not infrequently succeed, the flow of pitch being so great as to overcome and suffocate the beetles. Where the attacking force is large, however, the flow of pitch does not seriously hinder the beetles."

Figure 6 .—Attacks by the western pine beetle on a ponderosa pine may be indicated by "pitch tubes" in the bark crevices.

The Egg Galleries

Description

As the tree weakens and succumbs to the attack, the resin flow ceases and the beetles begin the extension of their egg galleries through the inner bark. These are winding tunnels a little larger than the diameter of the beetle. Hopkins (42) describes them tersely as "sub-transversely winding." The gallery very lightly grooves the surface of the sapwood and leaves a visible impression on the wood surface after the bark is removed due to stains left by the resins. Jeffrey (U103) states: "These galleries penetrate the cambium and inner living bark. When a choice is possible, the gallery is closer to the cambium side of the inner bark where the cell walls are not very thick." The parent adults keep several inches of the terminal end of the gallery, where they are working, free of sawdust which is carried back and packed in the completed gallery behind them. Surplus sawdust which cannot be packed into the tunnel is dumped out to the bark surface through occasional adits which the beetles cut through to the surface. These openings are known as ventilation holes. (See p. 51). The galleries form a network in the inner bark crossing and recrossing each other in the pattern peculiar to this species.

(Page 47a follows)

Figure 6.-- Attacks by the western pine beetle on a ponderosa pine may be indicated by "pitch tubes" in the bark crevices.

BEPQ 9806

Figure 7 .--Bark removed from a ponderosa pine killed by the western pine beetle exposes the winding criss-crossing egg galleries scoring the sapwood.

Noise of Construction

The chewing of the bark and wood by a great number of beetles extending their galleries is faintly audible. Keen (U126) states:

> "They produce a faint crackling sound like the crushing of dried leaves; a noise very similar, only more continuous and not as loud, as that made by cerambycid larvae when gnawing wood. In several instances, attention has been directed to infested trees which showed no outward sign of insect infestation through noise made by attacking beetles."

Miller (U189) in following an attack at Cascadel in 1925 recorded: "Noise made by the adult beetles in cutting their galleries could be heard. This noise was noted after 8 P.M. and before 6 A.M. as well as during the day, indicating that the activity within the tree does not die down at night."

(Page 48a follows)

Figure 7. -- Bark removed from a ponderosa pine killed by the western pine beetle exposes the winding criss-crossing egg galleries scoring the sapwood.

BEPQ 8567

Rate of Construction of Egg Galleries

The only record on this point was made in the Ashland studies. Keen (U126) observed on caged logs that the female was able to construct an average of 0.65 inch~~es~~ of egg gallery per day; also that a ventilation hole is constructed for about every 4 inches of egg gallery. This is probably the maximum rate of construction under favorable temperature conditions. It is known that the construction of egg galleries ceases with the advent of cold weather in the fall. Since the adult beetles become inactive at temperatures around 50° F. and lower, it can be expected that all activities connected with the attack slow down as the temperature approaches this point and that little or no work is done at colder temperatures. RTH

Position and Number of Egg Niches

After the female has extended the egg gallery a few inches from the entrance chamber, she begins to make tiny notches at frequent intervals along the sides of the egg gallery [to receive the eggs and it is in these notches that the eggs are deposited]. The~~se~~ notches have been described by Keen (U126):

> "The egg niches are located in the soft bark off the main gallery and separated from it by a wad of frass which is packed into the niches after the egg is deposited. Often when the bark is stripped from the wood, the eggs are visible in their niches, but more often they are concealed by the frass packing or a very thin layer of the phloem. The number and distance apart of the egg niches varies greatly with the different attacks and even in the same egg gallery being very irregular. Sometimes the eggs are only one-sixteenth of an inch apart and at other times there will be 3 or 4 inches of gallery with no eggs on either side."

From an examination of 210 inches of gallery representing 11 attacks on 111 trees, 591 eggs were found or an average of 3.4 eggs per inch of gallery.

Person (U229) examined 19 square feet of bark on 13 trees of the Cascadel area and counted 5,693 eggs in 1,363 inches of gallery or an average of 4.2 eggs per inch.

The general average from the counts made so far are therefore about 4 eggs per inch of gallery.

Total Length of Egg Gallery

On this point Keen (U126) states: "The maximum length of a gallery which any pair of beetles would form was not determined, but it was found from averages that beetles constructed at least 17 inches of gallery per attack and 187.8 inches of gallery per square foot of bark."

Measurements reported by Patterson (U209) from counts made by P.D. Sergent in the Jenny Creek area of Oregon showed averages ranging from 8.4 to 14.5 inches of gallery per attack. These measurements apparently were made while the extension of galleries was still in progress and before the beetles had completed the full length of excavation.

Person (U229) obtained an average of 131 inches of egg gallery per square foot of bark, from a count of 4 square feet or 10.9 inches per attack on the Cascadel area.

In 1941 Yuill (U336) in connection with a study of beetle behavior in high and low risk trees found an average of 156 inches of gallery constructed per square foot in samples from 80 trees. There was no difference between the high and low risk trees.

A summary of all of the data taken on this event shows a general average of about 14.0 inches of egg gallery constructed for each attack and about 162 inches per square foot. This of course is subject to wide variation with different densities of attack and the success of brood development.

Ventilation Holes

Hopkins (43) states:

> "Ventilating burrows are the vertical [sic] burrows located at frequent intervals in the roof of the egg gallery and extending outward to or near the surface. They are utilized by the parent adults as a place in which to turn around, or in which to pack the boring dust, or through which to eject the dust, as the case may be."

Subsequent observations and studies have confirmed Hopkins' statement as to the purpose of ventilating burrows in most respects. But it remained for Buckhorn (U39) to show that the real purpose of the open holes was not to ventilate the egg galleries or to discharge boring dust but to provide an exit for emerging parent adults. He states:

> "This finding was verified by careful observation throughout the season (1934). After construction of the gallery is under way, holes of various depths are bored by the parent adults into the outer bark. Many of these extend to but do not attain the outer bark surface. No openings are made through the surface until a parent adult emerges and leaves an open exit hole. No adult forms of secondary insects were noted to enter the D. brevicomis galleries until a parent adult had emerged and left an open hole as a means for their entrance. Prior to emerging the parent adults feed around in the inner bark. This feeding character can easily be recognized as a short section of the gallery is usually enlarged, forming a large chamber from which several short galleries may extend. These feeding places are always free from frass and are found at the base of the exit hole."

The number of ventilating holes per attack and per square feet of bark has been given attention in bark counts largely for the purpose of separating them from the count of new adult exit holes. In the "toothpick method" of making bark counts they have been separated from exit holes whenever a toothpick completely penetrated the bark from an egg gallery. (U174)

Bark counts on the Ashland area reported by Keen (U126) showed an average of 9 vent holes per square foot in an examination of 40.8 square feet of bark, and from an examination of 200 attacks, an average of 2.1 vent holes per attack. From an examination of 330 square feet of bark in the Rogue River area, Glendenning (U69) showed an average of 16.4 vent holes per square foot. Patterson (U209) in summarizing the bark counts made on the Rogue River area between 1914 and 1923 shows an average of 21 vent holes per square foot from an examination of 1857 square feet of bark. This number of vent holes is roughly in proportion to the number of parent adults found emerging per square foot of bark.

Re-Emergence of Parent Adults

Soon after gallery construction has commenced some parent adults may decide to leave their present location and seek more favorable opportunities elsewhere. They then bore out through so-called "ventilation holes." (See p. 51). As Buckhorn has shown, a few may emerge at any time after attack has started, but the majority remain under the bark and do not emerge at all or emerge later after the gallery construction has neared completion.

This habit of re-emergence was not noted by Webb (133), who reported that the parent adults remain in the galleries until they die, but re-emergence has been found in practically all subsequent studies dealing with the habits of the parent adult beetles.

Re-emergence of parent adults was first reported by Keen (U126), who caged a down log containing an overwintering brood composed of parent adults and eggs. A green log was placed in the cage to absorb any parent adult beetles which might emerge. These did emerge during March, April, and May, and reattacked the log. It was also noted that in the field parent adults were emerging at the same time before the new adults had formed. These attacks were largely confined to the base and uninfested portions of previously attacked trees. They were unsuccessful on green timber. From a count of 20 square feet of bark, it was determined that about 57.5 percent of the parent adults had emerged, and that this emergence had occurred "about the time the brood reached the three-quarter grown larval stage."

Furniss (U65) investigated the activities of re-emerged parent adults on the Modoc National Forest in 1933 by caging and forcing attacks on standing trees during the summer period. He found that:

> "1. Parent adult beetles emerged to the extent of 53.6 percent of the attacking population.
>
> 2. Parent adult emergence began when the progeny was about a quarter-grown, reached its peak when the larvae were half-grown and ceased just prior to the time that new adults emerged.
>
> 3. Re-emerged parent adults were capable of establishing a second brood which developed to maturity."

Buckhorn's studies (U39) on the Ochoco National Forest in Oregon showed that parent adults might emerge at any time after gallery construction started but showed a peak emergence about 15 to 18 days before the new adults start emerging.

Salman (U262) with the assistance of Bongberg made a very thorough study of the activity of re-emerged parent adult beetles on the Modoc area in 1934. Cages were constructed on newly attacked trees to trap the emergence of parent adults from each seasonal generation; these re-emerged adults were then forced to attack caged trees and the success of their attack determined. They found that:

> "(1) This season's work showed re-emergence to be a normal habit. Re-emergence followed the attacks resulting in the 3 primary generations of the 1934 season.

"(2) In the first generation emergence of parent adults from 20 caged trees ranged from 2.1 to 36.9 beetles per square foot and averaged 19.1. It was estimated that the re-emerged population had a force about one-twelfth (8.2 percent) as great as that of the adults emerging from overwintering trees.

"(3) In the second generation, re-emergence from 6 cages ranged from 4.8 to 42.0 beetles per square foot. It was estimated this re-emergence had had an effectiveness nearly one fifth (19 percent) as great per unit of bark surface as the progeny of the first generation.

"(4) In the third generation, which attacked in the fall, some re-emergence of parent adults occurred before cold weather set in, but it was considered that many of them which overwintered in the trees re-emerged the following spring.

"(5) The sex ratio of re-emerged parent adults was variable, but averaged 40.2 percent males and 58.8 percent females.

"(6) Pure attacks of re-emerged parent adults resulted in normal development and progeny in normal amounts.

"(7) A second re-emergence of parent adults was found to occur late in the season. These beetles had emerged for the first time as progeny from overwintering trees, attacked a standing tree from which they re-emerged, and attacked a second standing tree from which they made their third emergence. These beetles were very few in number.

"(8) Beetles which had made the second re-emergence attacked a caged log and produced a brood from which some small sized adults developed. Abnormal brood development was attributed to poor conditions in the trap log."

The complication of generations which developed from the re-emergence and attack of parent adults during the 1934 season on the Modoc National Forest is illustrated by diagram in Figure 17 on page 157a.

THE EGG STAGE

Description

The generic character of the eggs is described briefly by Hopkins (42). "The eggs of Dendroctonus have not been studied in detail, but they are short, oval to oblong-oval, pearly white and shining and apparently without distinctive generic or specific characters." No more specific description of the egg of Dendroctonus brevicomis is found anywhere in published literature or manuscripts.

Number of Eggs Per Female

In the early work at Ashland, Keen (U126) states: "the maximum number of eggs laid by any one female was determined as 41 with an average of 30." But he goes on to state that "this figure is undoubtedly too low, as it is difficult to get the complete egg laying capacity of a female without disturbing or injuring her in some way." By counting the number of eggs in a sample length of gallery and determining the inches of gallery per square foot, and the number of attacking females per square foot, Keen estimated 64.5 eggs per female and 93.6 eggs per attack. Reporting on 55 galleries counted by Sergent, Patterson (U209) gives the average number of eggs per gallery as 35.4.

On the basis of the general average of 4 eggs per inch of gallery and 14 inches of gallery per attack (see pages 50), the average number of eggs per attack should be about 56, and the average number of eggs per female, 48.

Like many other statistics of beetle habits, this one is subject to a wide variation due to differences in numbers of attack per square foot of bark, inches of gallery constructed, and egg laying capacity of different individuals. The averages can only be considered as indicative at best.

Period of Oviposition

"Commencing with the first eggs which are usually laid about 8 days after attack, egg laying continues from 10 to 49 days with an average of about 23 days. This egg-laying period, of course, is extended in the case of females which overwinter before depositing their full complement of eggs." (U126).

Incubation Period

Webb (133), referring to first generation trees at Centerville, Idaho, states: "These eggs hatch in about 4 days after deposition."

Chamberlin (17) states that "the eggs hatch in a week or 10 days." Struble (U285) in transferring individual eggs from the bark to petri dishes in a series of experiments noted that "the eggs in practically every instance hatched 1 to 5 days after transferring to petri dishes." Jeffrey (U103) states: "These eggs hatch in somewhat over a week." Person (U229) recorded 7 days from first egg to first larvae for the first seasonal generation, 8 days for the second generation.

In 1931 Beal (U6) made a laboratory study of the effect of temperature upon incubation. A series of recently laid eggs were isolated on moist blotting paper in covered petri dishes and exposed to constantly maintained temperatures with the following results:

At 60° F. - 20 out of 50 eggs hatched in 16 days.
At 55° F. - 14 out of 50 eggs hatched in 16 days.
At 53° F. - 7 out of 50 eggs hatched in 16 days.
At 40° F. - 0 out of 50 eggs hatched in 21 days.
At 36° F. - 0 out of 50 eggs hatched in 21 days.

This test was run primarily to determine the lowest temperature at which eggs would incubate and the results indicate the minimum temperature to be around 50° F. Beal states that "eggs hatched at approximately the same temperatures at which larval and pupal development began."

It is obvious from all of these observations that the rate of incubation of D. brevicomis eggs is regulated by temperature; that development begins just above 50° F. and is very slow up to 60°. Optimum temperatures under which incubation is completed in 7 days are probably between 70 and 90° F.

THE LARVAL STAGE

Description

The only technical description of larval characters was given by Hopkins (42). This is too long to be quoted here. In general appearance ~~the~~ larvae of the beetle are small, white, subcylindrical, wrinkled, curved, legless grubs about one-fourth of an inch long with a small yellow head. They may be found by slicing [half-way] through the bark of an infested ponderosa pine.

The Larval Mine

The larval mine has been described by Keen (U126): A quotation should not immediatel

> "The larva upon hatching commences boring its gallery at right angles to the egg gallery. The first one-eighth of an inch is usually under a small layer of the bark, then it goes deeper so that the bark is cut and the cambium reached, and sometimes the sapwood is faintly scored. After about half an inch or more of gallery, it returns to the bark or inner bark and commences working outward towards the outer bark. After about 7 days, it reaches the junction of the inner and outer bark where most of its development occurs. After it has nearly completed its growth, it bores further out into the bark and forms an enlargement of its gallery in which to pupate." [—Keen(U126)]

The mine is at first very tiny, being just large enough to accommodate the newly hatched larva; it steadily increases its size with the growth of the larva and is tightly packed with sawdust except for the outer end where the larva is feeding.

Figure 8 .—Typical winding egg galleries of the western pine beetle on the inner surface of ponderosa pine bark, showing the start of larval mines.

(Page 59a follows)

Figure 8 .— Typical winding egg galleries of the western pine beetle on the inner surface of ponderosa pine bark, showing the start of larval mines.

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Food Habits of the Larva

The larva must obtain its food from the cambium, phloem, and the outer bark because it does not go through its development in any other parts of the tree. These areas contain a number of organic substances, but just which ones are actually utilized in nutrition is a question that has not been definitely answered. Jeffrey (U103) suggests that it is the cambium area which supplies the most available larval food material because "in this part of the tree, tree growth is taking place and the supply of larval food material, especially proteins and simple sugars, would probably be greater than in the wood or outer bark."

During 1929 and 1930 interest in the nutritional requirements of the larva was stimulated by the theory that here would be found the explanation for the selection of certain trees by the beetles. It was thought that these preferred trees might have a high content of nutritional material compared to other trees that escaped attack. Struble (U285) attempted to determine what food elements are essential to development of the larvae by isolating individuals and feeding them in artificial media. It was planned to test certain organic substances in this way which were known to be important in the nutrition of other insects. These experiments were abandoned after a number of rearing media failed and it was found that the natural inner bark of the tree afforded the only conditions in which the larva could be carried through its earlier stages of development.

Jeffrey (U103) began an analysis of the organic materials found in the bark tissues in which the larvae feed. He pointed out that when the larvae are about one-quarter grown, they make a very abrupt and radical change in their environment and in the media in which they feed. "They move from the living bark (inner) which is comparatively soft and has a high moisture content (60 to 70 percent on the fresh basis) into the outer dead bark, which is very hard but non-fibrous and contains only 6 to 9 percent moisture."

At the time when the larvae migrate into the outer bark, they have by no means exhausted all of the inner bark tissue so that this does not explain the reason for this movement. Jeffrey did find an explanation, however, in the chemical changes that take place in the inner bark following the attack.

> "The natural medium in which *D. brevicomis* passes the critical parts of its life history is enormously more complex than that of either the termite or *Drosophila*. When the insect enters the tissue, the latter is alive. A mechanical injury, or girdling, is produced and micro-organisms of at least 2 kinds - yeasts and 'bluestains' (*Ceratostomella* sp.) --- are introduced. The girdling alone would be enough to cause a considerable change in the condition of the tree, but with the addition of the micro-organisms the change is enormous. In one log investigated by the writer, the total sugar concentration rose to twice the initial value, and subsequently dropped to one-twentieth of the highest value recorded. There was also a continuous change in the ratio of different sugars. The writer finds that by the time the larvae leave the inner bark the sugar concentrations there have fallen lower than in the outer bark to which they migrate."

These results of Jeffrey's work not only help to explain why the larvae migrate into the outer bark, but they also indicate that one important source of nutrition may be the unreduced sugars of the cambium, phloem, and outer bark.

Micro-Organisms Associated with the Larvae

Jeffrey's work also served to emphasize the importance of certain micro-organisms during the feeding period of the larvae; particularly a yeast, first brought to notice by Struble (U285) and Person (105). According to Person this yeast was "always present on the larvae and new adults of the beetle." At first this yeast was thought to be a *Torula*, but later was determined as *Saccharomyces pini* (Holst.) (see page 317). It produces fermentations in the inner bark very soon after the entrance of the parent adult beetle, and the young larvae begin their feeding in tissues where active fermentations of sugars are in progress. In fact, no development of larvae has been observed except in association with this yeast. Whether or not this is a true symbiotic relationship in which the action of the yeast on the plant tissues is necessary to make the material available as food for the insect was not determined.

The Larval Instars

As the larva grows it goes through periodic molts or instars during which it sheds both the soft larval skin and the hard chitinized head capsule. With each molt the body gains appreciably in size and the new head capsule that is formed is definitely wider. Although these changes have generally been known to occur it has been practically impossible to observe them because the larva throughout its development is concealed in its feeding galleries in the bark. The cast skins in the galleries are soon lost in the frass or eaten by other insects that inhabit the galleries.

It was not until 1934 that an attempt was made to determine the number of larval instars of the western pine beetle. The first work was undertaken by Salman (U260), who determined that the larvae pass through four instars. Further detailed work was reported by Salman and Bongberg (U265) who approached the problem by measuring the changes in head capsule widths during the development of broods in infested trees. By collecting infested bark at 2-day intervals, killing the larvae by boiling, and later measuring them, it was found that four distinct changes in head width occurred during the progress of development. The authors concluded that:

> "1. The western pine beetle passes through 4 instars in its larval development.
> 2. There is no indication of extra instars occurring in the development of some individuals or of one sex.
> 3. The larvae of the first instar are to be found in the phloem.
> 4. The larvae of the second instar occur in both the phloem and outer bark. Apparently the migration from phloem to bark takes place in this instar.
> 5. The larvae of the third and fourth instars are to be found in the outer bark."

Period of Larval Development

When western pine beetle larvae have a food supply available for their nutrition, they continue to feed and grow as long as they are subjected to temperatures under which they can maintain normal metabolism. Moisture requirements must also be maintained although changes in moisture conditions do not seem to affect larval development as immediately or as drastically as temperature changes. Most of the studies dealing with moisture and temperature requirements have been concerned with the larval stage.

The first observations on larval development revealed that growth under natural field conditions slowed down as cold weather came on in the fall; that the larvae remained practically dormant during the winter period; and that the normal rate of development was resumed as warm weather returned in the spring. It was also noted that when broods in infested outer bark were collected during the dormant winter period and brought under warm room temperatures of the laboratory, the larvae soon started developing and continued on to the stages of pupae, new adults, and emergence if the bark was kept under these conditions.

Webb (133) first recorded the period of time spent in the larval stage in trees of the first seasonal generation near Centerville, Idaho.

> "It would appear that the length of time spent in the larval state is from 31 to 35 days. Sometimes, however, a few individuals of this first generation, either from retarded development or other causes, do not go through their transformation with the rest of the broods, but remain as larvae all through the fall and winter, evidently changing to pupae the following spring - thus it may require from 300 to 390 days for the complete development and emergence of some individuals of the first generation."

In 1915-16, Keen (U126) obtained records of the period for larval development under natural field conditions in the Ashland areas. He made repeated examinations of the broods in a series of 23 standing infested trees and by averaging the time periods from hatching of the eggs to formulation of the pupae concluded that "these records show the larval development period to be about 30 days for the first seasonal generation, 60 days for the second generation, and 155 days for the overwintering generation."

Other records kept in 1918 by Miller (U173) on infested trees in the southern Sierra Nevada and some kept by Patterson (U205) in the Yosemite National Park in 1919 followed very closely the same rates of larval development as those recorded by Keen.

In 1926, from a series of 10 trees on the Cascadel area near North Fork, California, in which intensive records were kept on brood development, Person (U229) determined that the period from "first larva hatching" to "first pupa formed" averaged 20 days for both the first and second seasonal generations.

Furniss (U65) in following the development of larvae in infested trees near North Fork, California, found considerable difference in the period of larval development between generations and between seasons. His data can be summarized as follows:

Season	Period of larval development in days 1932	 1933
First seasonal generation	45	75
Second seasonal generation	34	75
Overwintering generation	165	--

The graph illustrating these records apparently refers to the average period during which the larvae of each generation were found in the trees and not to the development of individual broods. The difference between the two seasons was attributed to climatic variation.

> "The only apparent difference was in the cold period which followed the early warm temperatures. In 1932 the cold weather was sufficiently delayed for the first seasonal generation to become fully established. In 1933 the cold weather stopped the emergence of the overwintering generation before it had fairly begun and emergence did not begin again until a month later."

Temperature and Moisture Requirements

In these first field records no attempt was made to determine the actual range of temperatures under which the larvae were active, nor the low and high temperatures which limited their development. It was generally accepted that the temperature responses of the western pine beetle were similar to that of many other insects which become active at temperatures around 50° F. and reach their maximum activity under temperatures between 70 and 90° F. Little was learned concerning the moisture requirements of the beetle in these field studies.

It was not until 1929 that an attempt was made to determine with some degree of accuracy the temperature and moisture conditions that are most favorable to the beetle. During the season, Beal (U6) began a series of field studies in which he followed brood development in slash material in southern Oregon and measured the temperatures and moisture conditions under which this brood development took place. Beal's first work in 1929 to 1931 was limited to such variations of temperature and moisture as were found in the field and he made no attempt to regulate these factors.

Later in 1931, Beal moved these studies into the laboratory at the University of California, where temperatures could be controlled. Here he ran a series of experiments in which the rate of brood development could be followed in infested logs and bark sections in a series of insulated compartments with air temperatures regulated within a variation of plus or minus 2°. The temperatures maintained were: 35, 40, 48, 52, 60, 65, 70, 75, 85, 95, 100, and 106° F. Atmospheric humidity was regulated by ventilation and was not controlled. Moisture determinations of the bark and phloem were made at intervals during the progress of the experiments. The material used in these studies consisted of the following:

1. Log sections, in which a successful attack had been established with the parent adults and egg stages predominating, were placed under each of the maintained temperatures. Development of the broods was then checked at frequent intervals with less frequent determinations of moisture percent of the phloem and inner bark. The moisture percent was found to be high at all times, averaging from 200 to 300 percent in all logs except those kept at the highest temperatures, which had a slight tendency to dry out. It was found that brood development in most of the tests could be followed only part way through the larval stage because of high mortality which set in after a few weeks.

2. Selected mature larvae not yet in the prepupal stage were obtained by shaving up infested bark and were placed in outer bark sawdust and subjected to the same range of temperatures and moisture conditions as the log sections. The mortality which developed in these mature larvae was low and it was possible to follow their development through to the prepupal, pupal, and new adult stages.

3. Larvae, removed from the bark by the same method as for (2) were subjected to temperatures alternating between 40 and 75° F. for varying periods, and their development followed. This was to determine whether fluctuating temperatures corresponding to those under which development takes place in the field would result in responses differing from those obtained at constantly maintained temperatures.

The results of field and laboratory studies were summarized by Beal in his final report (U6).

"1. Brood development of this insect begins at about 50° F.
2. The rate of development increases directly with the temperature up to about 80° F.
3. Constant temperatures of 95° F. and above if sufficiently long maintained are fatal to all stages.
4. Most rapid development occurs at about 85°F., but the most successful development from the standpoint of greatest numbers of insects produced is in the vicinity of 70-75° F.
5. Phloem moisture of infested felled material increases or remains abnormally high in all cases except at high lethal temperatures where some drying occurs.
6. Failure of broods to develop at low temperatures below 50° F. and at high temperatures above 95°F. is probably due to the effect of limiting temperatures.

7. Brood failures occurring within favorable temperature zones are probably due to excessive moisture of the inner bark or some factor closely associated with it.
8. Daily changes in temperature appear to have no stimulating effect upon brood development.
9. A definite number of hour-degrees of effective temperature is necessary for the development of a specific brood stage of the western pine beetle."

Beal was unable in these studies to establish the total number of hour-degrees above 50° F. required to carry the larvae through from the egg to the prepupal stages. However, the results obtained by carrying mature larvae through to new adults furnished quite convincing evidence that the rate of development is dependent on accumulated hour-degree temperature above 50° F. "The hour-degrees obtained by the summation of alternating temperatures and the summation of different constant temperatures gave in both experiments about 10,000 hour-degrees for development of mature larvae to final adults."

In 1934 Salman (U262) undertook a program to determine whether the relationships between temperature and brood development already indicated by the laboratory studies of Beal and others could be confirmed by records in the field. The objectives, as stated by Salman, were to determine "the relationship of air temperatures to bark temperatures, and the temperature requirements of broods developing normally in the bark of infested trees." The application in mind was that a record of air temperatures, as made available by ordinary weather stations, could be used as an index to important seasonal activities of the beetle; and that seasonal events important in the timing of control work, such as the spring emergence, could be forecast with some certainty from weather records in the infested areas.

Salman was assisted by Struble, Furniss, and Bongberg in this series of studies which extended over a period of 3 years. Temperature and brood development were recorded in two localities with significant climatic differences; near North Fork representing low elevation west slope conditions in central California; and at Hackamore representing the high plateau conditions of northeastern California. Bark temperatures were measured by specially designed thermographs which gave a continuous record within the bark at the depth where larval development took place. These records were maintained in a series of trees at a height of 10 feet or more above the ground. In addition a series of temperature readings was secured from two trees by means of a potentiometer and thermocouples which compared air and bark temperatures at varying heights up to 80 feet above the ground. Brood development was observed by frequent examinations of infested bark and ultimate emergence was recorded by screening bark areas on standing infested trees to trap the adults as they emerged. Altogether about 50 infested trees were included in these studies.

In discussing the relation of bark to air temperatures under the range that occurs during the season of beetle activity, Salman made the following overall summary:

> "Perusal of bark temperature records shows that each tree has a characteristic curve. The characteristics of each curve have been found to be dependent, in part at least, on the hours during which sun strikes the bark surface.

> "On basic records from 6 trees there appears to be little possibility of correlating air and bark temperatures in small units such as hours or even days. However, weekly summations do show a distinct relationship. There are indications of a fairly constant response of bark temperatures to air in the mid range, a resistance to absorption of heat at higher temperatures, and a decided resistance to loss of heat at the lower ranges.
>
> "One point of importance brought out is that bark temperatures (accumulated) during a given day are higher than air temperatures. A temperature surplus is accumulated each day. On some trees this surplus is great, on others slight."

Yuill (U331) made a separate report on an experiment to determine the relation of air and bark temperatures at the base of the tree to bark temperatures at different heights on the main bole. These temperatures were measured by means of thermocouples inserted into the bark at the depth of developing brood stages. Comparative air temperatures were also read by thermocouples. Because of difficulties in developing a type of thermocouple adaptable to the bark, many important readings were considered unreliable. Yuill, however, considered the following points established:

> "a. Air temperature is the same at different heights along the trunk, except for a slight effect of radiation at the base.
> b. Probably due to radiation, the bark temperatures at the base of the tree reach slightly higher and lower extremes than those higher on the bole.
> c. Bark temperatures in areas exposed to the sun tend to rise above air temperature, and when shaded tend to revert to air temperature. There is considerable lag in these changes, so that the bark temperatures do not reach the lower extremes that air temperatures do.
> d. The warmest side of the tree lies between the west and south exposures.
> e. Where shade is not a modifying factor, bark temperatures recorded by a bulb-type thermograph at a given point are representative of the bark temperatures at other points on the same side of the tree."

On the relationship of brood development to air and bark temperatures, Salman did not consider the results satisfactory due to inadequate records of brood development. He was able to summarize in table form the hour-degrees required from first larvae to first pupae from one tree only. This shows a total of 7,127 hour-degrees for the entire period of larval development. Apparently because of the many variables encountered in the above studies, no attempt has been made to apply these results in the field by using temperature records as a basis for estimating the condition of brood development.

Larval Population

Glendenning (U69) in 1919 under J.M. Miller's direction, counted larval populations at Ashland, Oregon, by shaving 330 square feet of bark samples from a series of 67 infested trees containing overwintering broods of western pine beetle. Three or more samples of 1½ square feet each were taken on at least three sides of trees from 4 to 20 feet above the ground. These counts showed 185 larvae per square foot of bark in the advanced larval period from January 1 to April 1 and 122 per square foot in the prepupal period from April 1 to May 24.

Following the cold winter of 1932-33, 1143 bark samples were collected by rangers from 33 localities in eastern Oregon and Washington during the period January 1 to April 6, 1933, and sent in to the Portland Forest Insect Laboratory, where they were shaved, and the live and dead larvae carefully counted to determine the effect of the freeze. An average of 189 larvae were found per square foot in the 782 square feet of bark examined (Keen and Beal U144).

THE PREPUPAL STAGE

As the larva approaches the end of its feeding period, it makes an elongated cell at the end of its mine in the outer bark just large enough to accommodate the full grown stage. This cell is kept clear of borings, and here the larva goes through a resting period before it is ready to pupate. According to Salman and Bongberg (U267), "Just preceding pupation, fourth instar larvae enter a physiological condition that is known as the prepupal stage." As the larva passes into this prepupal condition, great changes take place in its body functions. Feeding ceases entirely and will not be resumed until the adult stage is reached. The body becomes soft and shows little reaction to stimuli. Internal changes take place preparatory tothe re-grouping of the body cells to form the entirely new characters of the ~~pupae~~ pupa and adult.

Description

Hopkins does not mention or describe the prepupal stage, and descriptions are lacking in published literature and in manuscript reports. Externally the prepupal larva still resembles the fourth instar, but it can easily be distinguished from the mature larva by certain characteristics of appearance and posture. The prepupal larva becomes sluggish and lies in a distended relaxed position, with head generally pointing toward the center of the tree, whereas the mature larva is active and curls up its body when disturbed. In color the prepupal larva is yellowish-white, while the mature larva is white or slightly pinkish-white. The prepupal larva is entirely opaque while in the mature larva ingested material in the alimentary canal can be seen in shadowy outline through the external skin. The thoracic segments of the prepupal larva tend to enlarge and show some differentiation from the abdominal segments.

Development and Temperature Requirements

Since this is an inactive stage during which the larva does not feed or move about in the outer bark, no particular events are connected with its development until the pupa takes form. However, the internal changes that take place preparatory to pupation cannot go on unless the prepupal larva is subjected to adequate temperature within its developmental range. The temperature requirements of the prepupal larva present an important departure from the temperature required for development of the younger larval stages.

All investigators who have followed the development of western pine beetle broods in the field have been puzzled by the absence of pupae during the winter period. It was found that where broods in the fall develop up to the mature larval stage, they rest at that point although broods still in the younger larval stages continue to develop. Furniss (U65) commented on this point.

> "The fact that most of the third generation passes part of September and all of October and November in the large larval stage while other stages were in the process of development is outstanding. Apparently prepupal larvae have a considerably higher temperature requirement for transformation than do the other stages of this insect."

In 1934 Whiteside (U321) made a thorough study of the temperature requirements for the development of prepupal larvae. He approached the problem in the laboratory by subjecting mature larvae removed from the bark to constant temperatures under controlled relative humidity of 55-66 percent. A series of constant temperatures ranging from 32 to 74° were included in the experiments. In his report Whiteside stated that the results indicated special temperature requirements for the change from the mature to the prepupal larva.

> "In the fall of the year, the physiological change from the last active fourth instar larval stage to the prepupal conditions acts as a bar or a barrier and prohibits the transformation to the pupal stage at a temperature near the zero of development (about 50° F.).

> "For mature larvae removed during the early fall, the zero of development lies above 50° and closer to 55° F. Once the prepupal condition has actually been attained, the metamorphosis to the pupal and thence to the callow adult stage will continue uninterrupted at temperatures as low as 45° F. Indications are that this phenomenon will take place at temperatures as low as 41° F.
>
> "For mature larvae removed during the early spring (February and March), the zero of development appears to be below 50° F., probably closer to 45°. A certain amount of feeding and development during the winter enables the larvae to transform rapidly to pupae and thence to callow adults with the rise of temperatures in the spring."

The period of time required for the transformation to pupae after the mature larvae go into the prepupal stage is relatively short under active temperatures. This is brought out by the tables in Whiteside's report presenting the results of a series of tests. These show considerable variation in time required, depending upon whether the larvae subjected to constant temperatures were removed from the bark in the fall or in the spring; but the period is probably best represented by a test started November 23 with larvae from an overwintering brood:

Temperature, °F.	Average period from prepupal larve to pupae: Days
74	2 ~~3~~
65	3
60	4
55	7

Whiteside records that when mature larvae were exposed at 50° a few pupae formed after 117 days indicating that some development does take place at this temperature. After the prepupal stage was reached, they transformed to pupae in about 18 days.

The greatest significance of the prepupal stage seems to lie in these temperature requirements which prohibit or retard development under the average field temperatures that set in with the beginning of the winter period. As a rule those larvae which have completed feeding in the fall go into the prepupal stage, continue into the pupal and new adult stages, and, if a few warm days occur, emerge before winter temperatures set in. Mature larvae which do not make the transformation to the prepupal stage rest in the outer bark until warmer temperatures arrive in the spring. In the meantime, younger larvae continue to develop during the warmer days of the late fall and winter until they reach the temperature bar for transformation to prepupae. Consequently there is a levelling off of brood development so that when warmer weather arrives in the spring, practically all broods are in the mature larval stage and ready to undergo the transformation to prepupae in mass.

THE PUPAL STAGE

Description

The transformation from prepupal larva to pupa takes place quickly without feeding or activity other than the internal and external changes that go on in the body of the insect. Hopkins (42) gives a technical description of the pupa, but no general descriptions appear in published literature or reports. Very close to the mature beetle in size, the pupa is white or creamy white in color; most of the appendages and external characters of the adult are present as pad-like masses of tissue; the abdomen extends well out beyond the wing pads and is characterized by noticeable soft spines; the entire body is soft and delicate and is incapable of movement except for spasmodic, rotation-like movements of the abdomen when the pupa is disturbed.

Development and Temperature Requirements

Under active temperatures, the insect does not remain long in the pupal stage unless long periods of low temperatures predominate. In trees of the first seasonal generation, Webb (133) found that "the length of time spent in the pupal stage is approximately 15 days." Keen (U126) followed the development of pupae in infested trees in the Lamb's Mine area and concluded that:

> "The records show an average duration period from larva to adult of 18 days for the first seasonal generation, with a minimum of 6 and a maximum of 38 days. For the second generation this duration period averaged 40.7 days, with a minimum of 13 days and a maximum of 92 days."

Miller (U173) and Patterson (U205) recorded the variation in the length of time during which pupae were present in individual trees as ranging from 7 to 20 days. Person (U229) in his Cascadel studies in 1926 recorded 8 days for the first seasonal generation, and 6 days for the second generation.

In his studies on pupation, Whiteside (U321) was able to follow a number of individual pupae through their transformation to new adults, and found that the period of their development varied with the constant temperatures to which they were exposed.

Temperature ° F.	Average days from pupa to callow adult
74	6
65	6
60	12
55	24
50	51

This record confirms the first observations of Keen and others that under conditions favorable to development, the minimum time in which pupae can complete their development is about 6 days.

Salman and Bongberg (U267) in summarizing individual trees' records for the Modoc areas state:

> "There are 18 records available concerning the time required for completion of development under field conditions. These indicate from 6 to 38 days are required. In May, from 10 to 29 days were required. In late July, August, and early September from 6 to 18 days were spent in the pupal stage."

THE CALLOW ADULT STAGE

Description

In manuscript reports, the term callow adult has been used to designate the stage that immediately follows the pupa in which the appendages and organs of the adult have taken form and free movement of the beetle becomes possible. The callow adult differs from the mature beetle mainly in the nature and color of the external shell. This shell is not fully scleritized and is still soft in the callow adult; at first it is yellowish in color and gradually changes to brownish yellow as the hardening of the chitin advances. The shell of the beetle when finally mature is dark brown to black in color.

Development

The change from callow adult to the mature beetle takes place gradually. The beetle remains in its pupal cell while the hardening and coloring process is going on, and does not start to bore outward until nearly mature.

In the available reports we find no record of studies to determine the time that the new adult spends in the soft-shelled immature condition of the callow adult. It has apparently been considered a relatively unimportant phase of the insect's development that precedes emergence. Brood records from the studies that have been made indicate that the callow adult stage has been lumped in with the records on new adults during the pre-emergence period.

THE PRE-EMERGENCE PERIOD

Duration of Period

Webb (133) noted that the new beetles, even when they have become fully chitinized and apparently mature, rest for a period before they leave the infested tree.

> "When first transformed in May and June, the young beetles have very soft delicate tissues. They therefore remain in their pupa cases until their bodies are fully hardened or chitinized. When nearly ready to emerge, the adults bore their way almost to the surface of the bark, but pause before emerging, appearing to rest in the burrows they have just made. The length of time spent in the bark after reaching this stage (adult) appears to be from 7 to 14 days."

The period spent by the adult beetle in the outer bark before it emerges was also recorded in the Ashland studies in 1916. (Keen, U126):

> "The adult event period or the time between the maturing of a beetle and its emergence averages 18.2 days for the overwintering generation and 7.1 days for the first generation. The duration and event periods are prolonged in the spring and accelerated in the fall."

Subsequent studies have not given attention to this phase of the adult's existence.

EMERGENCE

The act of emergence when the beetle comes through the last scales of the outer bark was first described by Webb (133).

> "When quite ready to emerge the beetles continue their burrows out through the remaining portion of the bark. The individuals of a brood do not appear to emerge simultaneously, but they come forth at irregular intervals until all are out, leaving the bark thickly punctured with small round clean-cut holes."

Period of Emergence and the Influence of Temperature

Keen (U126) states: "The emergence of beetles from a tree extends over a considerable period of time and is not concerted. A few hot days will cause the beetles to leave the tree in swarms, while a week of cold weather will almost completely stop emergence." He records the average period between the first and last emergence (from the same tree) to be 38.5 days; and he found straggling emergence in one case to extend this period to 99 days. Hopping (50) reports a few Dendroctonus holding over in abandoned trees and not emerging until the following year.

The temperature factor undoubtedly accounts for the lag in emergence of overwintering broods from the north side of a tree as compared with the south side. The north side is shaded while the bark on the south side may be warmed by the sun. Evenden (U57) records an average difference of 12.2 days in the final emergence between the north and south sides from a series of 12 trees near Coeur d'Alene, Idaho. Miller (U169) in summarizing the records of Keen and others in the Ashland areas states:

> "Overwintering broods in the south side of a tree may emerge from 27 to 41 days earlier than on the north side of the same tree; the average is 35 days earlier. Broods in trees of the first seasonal generation which emerge during the summer months and do not overwinter appear to develop at about the same rate on all sides of the tree."

Furniss (U61) noted this lag in emergence on the north side of trees near North Fork, California, in 1932 as ranging from 21 to 68 days.

Buckhorn (U38), who used cages to trap the emergence of beetles from infested trees on the Ochoco National Forest in central Oregon reported: "Since the emergence records were taken at about 7-day intervals, it was not possible to determine any small variations due to exposure on the tree. The emergence started and ended on approximately the same collection dates, but the peak of emergence from the south side of trees occurred about 8 days earlier than on the north side."

Although it has been definitely determined that emergence of adults of a generation of beetles may extend over a fairly prolonged period, quantitative records have shown that the great bulk of the population emerges in well defined peaks lasting only for a few days or a week. These peaks of emergence usually coincide with the first days of warm weather following the pre-emergence period and they may be abruptly interrupted by a spell of cold weather. Salman (U262), who followed emergence in the Modoc areas in 1934 found that "emergence of the main group of second generation trees (overwintering) occurred in 2 peaks, 1 during the middle of May and the other during the middle of June."

The Modoc emergence records obtained by maintaining traps on both overwintering and summer brood trees during the seasons of 1933, 1934, and 1935, were summarized by Salman and Bongberg (U267). A comparison of the three seasons was presented in graph form showing the relation of beetles emerging per square foot of bark to daily air temperatures (Figure 9). For all three seasons there were two definite peaks of emergence from the overwintering trees, but the periods when these peaks occurred varied greatly. The season of 1934 was about a month earlier than 1933 or 1935 in the emergence from both winter and summer trees. The season of 1935 was marked by late emergence extending well into November. The authors reached the following conclusion from these results: "Emergence starts as a result of temperatures that are frequently 60°F. and above; emergence generally ceases soon after maximum temperatures are frequently below 60°F. These statements are but rough rules of thumb based on 3 years of records."

Figure 9 .--Western pine beetle emergence in relation to air temperatures. Modoc National Forest, California. Seasons 1933, 1934, and 1935.

(Page 86a follows)

Exit Holes

The clear-cut exit hole~~s~~ that the beetle leaves in the bark surface as it emerges has been the subject of considerable attention on the part of investigators who were interested in population estimates. Since most new adults bore directly out from their individual pupal cells in the outer bark, the number of exit holes per unit of bark surface has been taken to represent the number of adults emerging from it. As a result, the exit holes have been counted in hundreds of bark samples to arrive at estimates of the numbers of beetles which took flight in certain areas. Ventilation holes have been separated from exit holes in these statistics. In summarizing these counts up to 1928, Keen (U138) emphasized the great variability in the number of exit holes per square foot of bark surface, - from 0 to 340 per square foot, with a mean of 63.

Salman, referring to studies in 1934 in northern California states: "Recent work has shown counts (of exit holes) give results considerably lower than actual emergence." (U262)

Buckhorn (U39) in comparing the averages for trapped emergence of beetles with exit holes in the same bark surface reported that:

> "The least number of beetles per hole was .4 and the highest 3.0, while 1.3 and 1.4 beetles per hole emerged most frequently. The 8 cases in which less than 1 beetle emerged are unaccounted for. This may be a natural phenomenon or due to beetles escaping from cages or getting lost or destroyed before collection."

The average emergence was 1.46 beetles per exit hole.

It is obvious that exit hole counts cannot be used to indicate the exact number of emerging beetles, but they can serve as a satisfactory index to emerging beetle populations. Consequently, the ratio of attacks to exit holes has been generally used in population studies as an indication of brood success.

Figure 10 .--Bark showing exit holes of western pine beetle and a larger [deep] hole drilled by a woodpecker in search of wood boring larvae.

THE TOTAL BROOD PERIOD

Time Required for Development from Egg to Adult Emergence

The time required for full brood development from egg to adult emergence is, as expected, subject to wide variations. This is dependent largely upon the seasonal generation involved and the climatic conditions of the locality where the records are [were] obtained. These differences in the time for the total brood period reflect the temperatures to which the broods are [were] exposed during development.

At Centerville, Idaho, Webb (133) records one tree in which "eggs were deposited July 6 and the broods developed and emerged by August 28, a period of 53 days." However, in the case of overwintering broods, "It may require 300 to 390 days for the complete development and emergence of some individuals."

(Page 88a follows)

Figure 10.-- Bark showing exit holes of western pine beetle and a deep hole drilled by a woodpecker in search of wood boring larvae.

larger

BEPQ 9356a

For the Lamb's Mine area in southern Oregon, Keen (U126) determined that the average brood period from first egg to first adult emerging for the first seasonal generation was 63 days; for the second or overwintering generation, 279 days. The minimum brood period from egg to adult emerging was 31 days; the maximum, 304 days.

For the Cascadel area, Person (U229) found that the period from first egg to first emergence averaged 46 days for the first seasonal generation in 1926; 38 days for the second generation; and 243 days for the third or overwintering generation.

Salman and Bongberg (U267), reviewing the results of three years of studies, stated: "The variations in the life history that are the result of the influence of temperature are so great that any definite statement of the time necessary to complete the life cycle will be of little use if expressed, without qualifications, in terms of days."

Beal (U6) in one experiment succeeded in carrying through development from egg to a single callow adult at a constant temperature of 93-97°F. This development was completed in 28 days. While this one case undoubtedly represents abnormal conditions, it is the shortest period yet recorded for completion of the life cycle and probably represents the minimum period during which it is possible for the western pine beetle to pass through all the stages of egg, larval instars, pupae, and finally reach the adult form.

Total Brood Production

From 1914 to 1936 a number of workers examined and made counts on hundreds of square feet of bark. The object was to determine the number of beetles needed to attack and kill trees and the resulting emergence under varying conditions and from year to year. It was hoped that these counts would determine the beetle's potential capacity to increase, what factors held it in check, and whether or not the success of brood production could be used to indicate trends of timber mortality.

Keen (U138) summarized the results of the brood statistical work done in the Rogue River and other southern Oregon areas between 1914 and 1926 which covered the examination of 979 trees and 4,177 square feet of bark.

The general averages for attack and emergence shown by these counts were as follows:

	Range	Median Value	Standard Deviation
Attacks per square foot	1 - 40	11.6	6
Exit holes per square foot	0 - 340	63	50

In this summary Keen emphasized the great variability which occurs in counts of different beetle events and particularly counts of attacks and emergence. "Attacks range from 1 to 40 per square foot of bark, with a mean usually falling between 6 and 12. It requires the examination of about 324 square feet of bark to obtain an average attack figure which is accurate within ± 1. Emergence counts show a tremendous variation, with a range of 0 to 340 beetles emerging per square foot (of bark) with no central tendency or mode. In order to obtain an average emergence with a maximum error of ± , 22,500 square feet of bark would have to be examined."

In order to obtain a figure for normal emergence of less variability than that derived from previous studies, to compare with emergence as affected by cold weather, Beal (U12) took a series of samples from three areas in eastern Oregon, including 37 trees and 579 square feet of bark. These samples were restricted to a band around the mid-bole of trees showing a normal attack by *D. brevicomis*; usually 15 to 25 feet above the ground, to trees of average bark thickness, and between 16 and 30 inches in diameter. Enough counts of exit holes per square foot were made on an individual tree so that the addition of three more samples did not change the general average more than ten percent. Similar counts were made on enough trees so that the addition of three more trees did not change the average for the area by more than ten percent. Usually from 15 to 20 samples were sufficient for each tree and likewise 15 to 20 trees proved to be ample for each area covered. With samples so restricted, the average number of exit holes per square foot was determined to be 112 for 1930 and 1931 overwintering trees with a standard deviation of 34.

During the years 1933, 1934, and 1935, W.J. Buckhorn (U38, U39, U40) carried on biological studies of D. brevicomis on the Ochoco National Forest in Oregon in which cages covering two square feet of infested bark were placed on the north and south sides of a series of trees at heights of 6 to 8 feet above the ground. Insects emerging were caught in jars partly filled with water and were collected at weekly intervals. The actual emergence of D. brevicomis recorded from this portion of the infested trees was recorded by seasons as follows:

Season	Bark Caged Sq. Ft.	Total D.b. Emergence	Average Emergence Per Sq. Ft.
1932-33	96	5,609	58.5 1/
1933-34	132	18,501	140.0
1934-35	120	13,255	110.5
Total	348	37,365	107.3
Total 2/	252	31,756	126.0

1/ Brood partly killed by the cold winter of 1932-33.

2/ Total excluding season of 1932-33.

During the period 1930 to 1934 considerable work was done on the Sierra and Modoc National Forests in California in caging bark and determining actual emergence. Salman (U262) summarized these data. From 974 square feet of bark caged the average emergence was 111 beetles per square foot. The variation in average emergence by generations was from 78 to 194 beetles per square foot and this was considered to be significant of population trends.

From these various studies a fair general average for normal emergence would be about 115 beetles per square foot. This in contrast to an average of 25 beetles attacking per square foot shows a normal population increase of about 5 times, in one generation.

Summary of Brood Statistics

All of the work done in making bark and brood counts has indicated such wide variations in all beetle statistics that few averages have been tied down within exact limits. Recognizing the limitations of any figures now available, the best average figures derived so far are as follows:

Brood Event	Basis Bark Sq.Ft.	Reported by	Average Per Square Foot of Bark
Number of attacks	4,177	Keen[4]	11.6
Number of parent adults attacking (2.1 per attack, 54% females, 46% males)	52	(p. 45)	25
Number of eggs (4.0 eggs per inch of gallery x 162 inches per sq. ft.)	25.7	Keen[3]	648
Number of larvae (overwintering Jan. 1 to April 1)	927	Glendenning[5], Keen & Beal[6]	188
Number of larvae (prepupal April 1 to May 24)	185	Glendenning[5]	122
Number of exit holes	4,177	Keen[4]	63
Number of exit holes (restricted sample)	579	Beal[7]	112
Ventilation holes	1,857	Patterson[11]	21
New adults emerging			
(Estimated from 1.46 per exit hole) Buckhorn[8] x 63 Keen[4]			92
(From cage records)	252	Buckhorn[9]	126
(From cage records)	974	Salman[10]	111

[3] Keen's report of Ashland studies (U126)
[4] Keen's summary of bark statistics (U138)
[5] Glendenning's bark counts of 1919 (U69)
[6] Low temperature studies, Keen & Beal (U144)
[7] Low temperature study, Beal (U12)
[8] Buckhorn's Ochoco caging studies (U39)
[9] Buckhorn's Ochoco caging studies (U40)
[10] Salman's summary for caging studies, 1930-1934 (U262)
[11] Patterson's summary of bark counts (U209)

TROPISMS OF NEWLY EMERGED BEETLES

The emerging beetle enters an environment entirely different from that in which it has spent all of its previous existence. Out of a micro-climate in the bark where light and air movements have been largely excluded, it suddenly finds itself in a world of ever varying light intensities, air currents, and odors in the surrounding forest. Relieved of the circumscribed conditions of its larval and pupal existence, it can now of its own volition or in response to stimuli choose the direction it may take in search of food and mate.

Its tropisms may have much to do with the time, direction, and distance that beetles fly before attacking another tree. The factors which have been given most consideration to date are its response to light, air movements, and attractive or repellent odors.

Light

Gordon (U71), who studied the tropisms of the beetle, stated: "The western pine beetle is positively phototrophic and negatively geotropic."

However, it does not require any special apparatus to find that the beetle after emergence crawls or flies toward the source of light and that under most conditions its first impulse is to move upward.

The first investigators soon found that when beetles emerge from a piece of infested bark which had been brought into the laboratory, they first move to the lighted windows; and if they cannot escape, they will remain on the glass or screen for several days. Also it was found that if the outer surface of the infested bark faces the light, the beetles come out through the outer surface as they do nn the standing trees; but if the bark is turned with the inner surface toward the light, the beetles reverse their normal direction of emergence and come out through the inner surface. However, if the bark is kept in a container with light excluded, it has been found that the beetles emerge from both outer and inner bark surfaces, apparently taking the shortest way out.

The fact that the emerging beetles go to the lighted windows might be attributed to their desire to escape from uncongenial surroundings in the laboratory. But experiments with emergence cages placed around trees in the forest have indicated that the movements of the beetle for some days after emergence are influenced by its urge to move toward the light. In several field experiments by Patterson (U206), Person (U229), and Miller (U189), screen cages were erected around the base of standing green trees and a quantity of newly emerged beetles were liberated within the cage. The results incidentally brought out the fact that when the beetles were first liberated, they went to the lighted walls of the cage and showed little interest in the enclosed living tree. Although enclosed under conditions which permitted considerable air movement and access to their natural food, the beetles were first drawn to the point of greatest light intensity on the cage walls. The same tendency was observed by Keen (U126). Both Miller and Keen record that this behavior persisted for 3 days. Eventually, however, most of the beetles confined in cages attacked the enclosed trees or logs after spending several days in an apparent attempt to escape toward the light.

One unreported phase of Gordon's laboratory studies on tropisms indicates that the beetles do not fly at all unless stimulated by light. About 300 beetles were liberated in a room from which all outside light was excluded. The temperature of the room was maintained at about 75°F. and it was lighted by a 75 watt ceiling light. Most of the beetles took flight under these conditions, and it was noted that the flight activity centered around the light. The beetles did not fly directly into the light, but would fly toward it, then past it. The direction of flight was erratic, followed no fixed direction, and was frequently reversed. But most of the beetles flew within a zone of 2 or 3 feet from the light itself. When the light was suddenly switched off, leaving the room in total darkness, the beetles could be heard dropping to the floor or striking the walls. When the light was switched on again after a few minutes, all the beetles were found resting quietly on the floor. Most of them resumed flight after the light was switched on again. This was further verified by Callaham's experiments in 1951 (U48).

This experiment of Gordon's serves to explain why we find no record of western pine beetle flight during the night hours, and why no one seems to have found them attracted to night lights in the vicinity of forest areas. We can only assume that during the flight period, they spend the night resting in bark crevices or on the forest floor. Observations on trees under attack indicate that the beetles fly to the trees only during daylight hours, beginning soon after sunrise.

These observations all point to a very positive attraction to light by newly emerged beetles. However, no one seems to have taken the time to determine the reaction of the western pine beetle to light during the pre-emergence period. Hensill (U93) tested the light tropism of mountain pine beetle adults which had been removed from logs before they had emerged naturally, and found that they were negatively phototropic to a very marked degree. Callaham (U47) found that the Jeffrey pine beetle was similarly negatively phototropic when adults were prematurely removed from their pupal cells. It is altogether probable that the immature adults of the western pine beetle possess the same response, since the avoidance of light would seem to be one of the factors that cause them to remain in the bark until they are fully matured and ready to emerge.

Whether the attraction of mature adults of the western pine beetle to light persists until the time they are ready to start new attacks was tested by Struble. (U293). In this experiment trap logs were exposed to the attack of beetles confined in a laboratory room. The light intensity for each log varied according to the distance from fixed windows. He found that the heaviest attacks occurred on those logs which received the greatest amount of light near the windows. Logs in the darkest locations drew only a very slight attack, but some attacks did occur on all logs regardless of their location.

Air Currents

Gordon (U71) conducted one experiment with his olfactometer in which he tested the reaction of the beetles to air movement alone. This was carried out under conditions in which the beetles could move only by crawling, since the air space in the apparatus did not permit of free flight. "A preliminary test with 180 beetles showed that 138 went against slight air currents (3 liters of water suction per hour). However, when the air current was appreciably increased above this value, contradictory results were obtained."

Callaham (U48) carried out studies of the olfactory and air current tropisms of the western pine beetle at Placerville in 1951 by using a specially designed wind tunnel. He found that with wind velocities up to one-half mile per hour, the beetles fly with the wind, and are unable to fly against it even in response to their strong phototropism.

Such field observations as have been made do not shed much light on the response of the beetles to air currents. Keen's observations in 1916 (described under "flight behavior") were that the beetles followed the direction of the wind. Evenden and Person do not mention air movement in their observations on flight, but Person states that the beetles took flight always in one direction; obviously this tendency could be due to other stimuli than air currents.

The general movements of populations in pine areas, as indicated by the location of infested trees, do not show a tendency on the part of the beetles to fly always with the prevailing winds. This is to be expected if odors are a dominant factor in drawing the beetles to the trees that they attack. It has been found that flight movements of the beetle are short and spasmodic. As winds usually change direction or die down within a 24-hour period during the flight season, they probably do not greatly interfere with the beetles' direction of flight or the distance covered.

Odors

Beetles apparently do not attack trees indiscriminately, but, regardless of the source of light or the direction and velocity of air movements, will avoid some trees in order to attack others. This observation has led to the assumption that responses to odors were a dominant factor in the beetles' selection of trees. If selection could be explained by some chemotropic response, then the beetles were undoubtedly able to recognize the odors of certain attractive trees to which they were drawn. Such odors might well be too faint to be detected by the human sense of smell, but still be recognizable to the highly developed olfactory sense of the beetle.

The study of this phase of the beetle's habits was stimulated by the theory that if the chemical nature of this attraction could be identified, then it should be possible to put the responses of the beetle to good use in control measures. If the odor could be produced synthetically, then it should be possible to attract the beetles to artificial traps in the forest after the manner of fly traps. The possibility of taking advantage of the beetle's tendency to select certain types of trees or materials led to a series of studies and experiments dealing with attraction.

The other possibility was that the beetles were not attracted by any distinctive odors or other emanations from particular trees; but in attacking more or less indiscriminately found certain weakened or felled trees more susceptible and readily killed and hence concentrated their efforts on these trees. This approach was more fully explored later in the studies reported under susceptibility and resistance of host trees (page 334).

Results of Attraction Studies

The Ashland Studies, 1916

In 1916, Keen (U122) summarized notes on the types and condition of trees infested by western pine beetle on the Ashland area. He found a variable degree of selection of fallen trees (windfalls), trap trees (recently felled), top-killed trees, trees infested by *Ips confusus*, and healthy trees in the vicinity of weakened trees. 26.6 percent of the abandoned top-killed trees and 26.2 percent of the trees still infested by *Ips confusus* on the area were attacked by *D. brevicomis* during the season. This was a much higher proportion attacked than for normal standing trees, and was considered to indicate a definite attraction on the part of the beetles for top-killed trees and those recently attacked by *Ips*.

The Cascadel Studies, 1926-1927

Person (U229, U232) started attraction studies in 1926 on the Cascadel area near North Fork, California. His first approach was entirely empirical, pointed toward finding any evidence that indicated that the beetles were being attracted to certain materials or to trees under varying conditions. Person had already established that the beetles selected the slower growing trees in the stand and he developed the following leads during the 1926-27 season:

Trap trees.— Beetles were readily attracted to and attacked freshly felled trees (traps) in one case, but failed to attack another. Factors governing attraction to trap trees appear to depend upon time of cutting, location, and characteristics of the tree itself. (See p. 598).

Top-killed trees.— Trees previously top-killed by *Ips* were found to be attractive to the western pine beetle. Out of 176 ponderosa pine which had been topkilled on the experimental area in 1924-26, 43 percent were attacked by *D. brevicomis* within 2 years after topkilling.

Artificially topped trees.— A series of 20 trees were artificially topped; a few of these attracted *D. valens*, but none were attacked by *D. brevicomis*. Artificial topping, therefore, seems to differ from *Ips* topkilling in its attraction to *D. brevicomis*.

Girdled trees.— A vigorous tree was girdled at breast height by removing a 2-foot band of outer bark, phloem, and cambium to the depth of the sapwood. This tree did not attract *D. brevicomis* until the second season following the girdling operation, when it was attacked and killed. (See p. 597)

Trees attacked only at base under cage conditions.— Beetles were attracted to both susceptible and resistant trees on which an attack has been artificially induced. This was demonstrated by a series of cage experiments in which 10 to 15 feet of the lower bole was screened in and adult beetles were introduced and forced to attack within the cage. In all cases, other beetles flying in the area were attracted to the tree and attacked it above the cage.

Roots injured by pruning.— Two fast growing trees which were heavily root pruned attracted *D. valens*, but did not attract *D. brevicomis* the first year after injury.

Lightning scars.— The observation that lightning-struck trees are usually attacked by *D. brevicomis* suggested that this attraction might be due to the result of over-heating freshly exposed phloem and cambium. Four trees were therefore artificially scarred to simulate lightning injury. A scar 2½ inches in width and extending from a point near the top of the trees to the base was made on each tree, two of which were slow-growing and two fast-growing. Two of the scars were scorched with a blow torch. None of these artificially scarred trees attracted *D. brevicomis*, but a few *D. valens* did attack one of the trees near the base. As a group of 3 trees situated within 100 feet of the experiment were attacked and killed, the failure to get attack on the scarred trees was not due to lack of beetles in the vicinity. (See p. 366)

Fire injury to foliage.— In April 1927 just prior to the flight period, a series of 9 trees were artificially scorched with varying degrees of injury to the foliage. None of these attracted *D. brevicomis* until September, when 2 trees, which had been 100 percent defoliated, were attacked and killed. This experiment confirmed the result of other studies that the odor of smoke or recently fire-scorched trees does not attract *D. brevicomis*. However, the effect of fire injury in suppressing subsequent growth does attract the beetles to severely defoliated trees within a year or two after the injury. (See p. 455)

Pitch masses.— The results under the above suggested that the pitch flow produced by attacking beetles was the source of attraction. Person then transferred pitch tubes from an attacked tree to 3 selected unattacked trees of slow growth rate. Two new attacks were made near the pitch masses on one of these trees, but the attacks were unsuccessful. In 1927, pitchtubes were placed on a very slow growing tree which was later attacked. The general results indicated that the pitch masses may have some attractive influence, but that it is too slight to be of great significance.

Beetles boring in phloem area.— It was next considered that the attraction might be due to the presence of adult beetles themselves when working in fresh pitch flow. Person, therefore, started a number of beetles into selected trees by first making a nail hole into the phloem and introducing beetles; about 20 percent of the beetles introduced in this way attempted to extend egg galleries into the trees, but were unsuccessful. In the case of one slow growing tree, these attacks through the nail holes were followed by a successful attack over the entire bole from beetles flying in the area; but here again there was a question whether the general attack had been induced or would have occurred anyway.

Concentrations of beetles.— Studies were made to determine the attraction of a large concentration of adult beetles to other beetles flying in the vicinity. This was done by observing evidence of attraction to the emergence cages where large numbers of beetles were confined and to adjacent trees. No evidence was found to indicate that any such attraction occurred.

The Modoc Studies, 1928-1929

In 1928 Person transferred the Cascadel attraction studies to the Modoc National Forest in order to carry on the project in an area where there was an active epidemic infestation and large areas of susceptible timber. During 1928-29, he carried out a comprehensive series of experiments to determine the attraction of the beetle to different parts of the trees, to slow growing as compared to fast growing trees, and to various chemical substances. In this work Person was assisted by Mirov, who worked on the chemotropic responses of the beetle, and by Jeffrey, who studied the changes that take place preceding and subsequent to attack in the sugar concentrations of the bark and phloem.

Mirov (U202) made a very intensive study of the reactions of the beetle under insectary control to attractive and non-attractive materials. A large screen insectary was constructed for this study. The beetles were reared in large numbers in separate cages and then liberated in the insectary. Specially devised traps were used in the insectary to trap the beetles coming to attractive materials. Mirov's report reviewed the literature of previous work that had been done on the chemotropic responses of insects, in addition to presenting a number of significant conclusions developed by his own experiments with the western pine beetle. Among the latter were the following:

> "It was soon found that insulation, relative humidity, and temperature play a very important part in attraction studies. (Especial measures were taken in the insectary experiments to compensate these factors.)
>
> "*Dendroctonus brevicomis* is positively chemotropic towards *Pinus ponderosa* and is attracted by odoriferous substances emanated by its host tree.
>
> "Sugars present in the phloem of *Pinus ponderosa*, and probably products of their decomposition, have been found to be more attractive than essential oils of bark and wood. Essential oils of needles proved to be non-attractive to this beetle.
>
> "Fermented phloem proved to be the most attractive of all the materials used.
>
> "It has been found that there is quite a pronounced preference in the olfactory response which *D. brevicomis* shows toward slow growing trees, especially to the phloem. This item needs further study."

Mirov did not continue these attraction studies in 1929, but Person and Jeffrey developed further phases. Jeffrey's work (U102, U104) on phloem and bark sugars showed that the concentration of reducing sugars - particularly levulose - is higher, and that the sucrose concentration is lower, in the slower growing attractive trees than in the faster growing less attractive trees. (Figure 11). When a tree is felled, changes in sugar concentration set in, such as would be associated with fermentation. This is followed by a rapid decrease in sugars, evidently caused by respiratory fermentation produced by micro-organisms. (Figure 12) Jeffrey states (U102):

> "It is not intended to suggest that the actual hydrolysis of sucrose to reducing sugars in either the standing slow-growing tree or the felled log would actually attract beetles. It is a definite possibility, however, that some other change associated with or following this change might produce a volatile substance which would be directly attractive to the beetles."

Figure 11 .—Relation between growth rate and the concentration of certain sugars in the living bark of ponderosa pine.

Figure 12.—Changes in concentration of certain sugars in the living bark of ponderosa pine following felling and western pine beetle attack.

Still another line of attack upon the factors involved in attraction was the relation of hydrogen ion concentration in pine phloem, or pH, to bark beetle attack. A preliminary exploration in this field was made by Houghton Durbrow (U51), working under the direction of H.L. Person on the Modoc areas. The plan of this study was to compare the pH in trees from different vigor classes to see if there was any correlation between pH and bark beetle attack. The study did not get much farther than working out the technique for determining the hydrogen ion concentration in the phloem, and very little was established to show that this is an important factor in the attraction of bark beetles. Durbrow's conclusion was that "apparently pH is not a satisfactory index to the health or attractiveness of trees." However, he summarized the available results as follows:

(Pages 109a,109b follow)

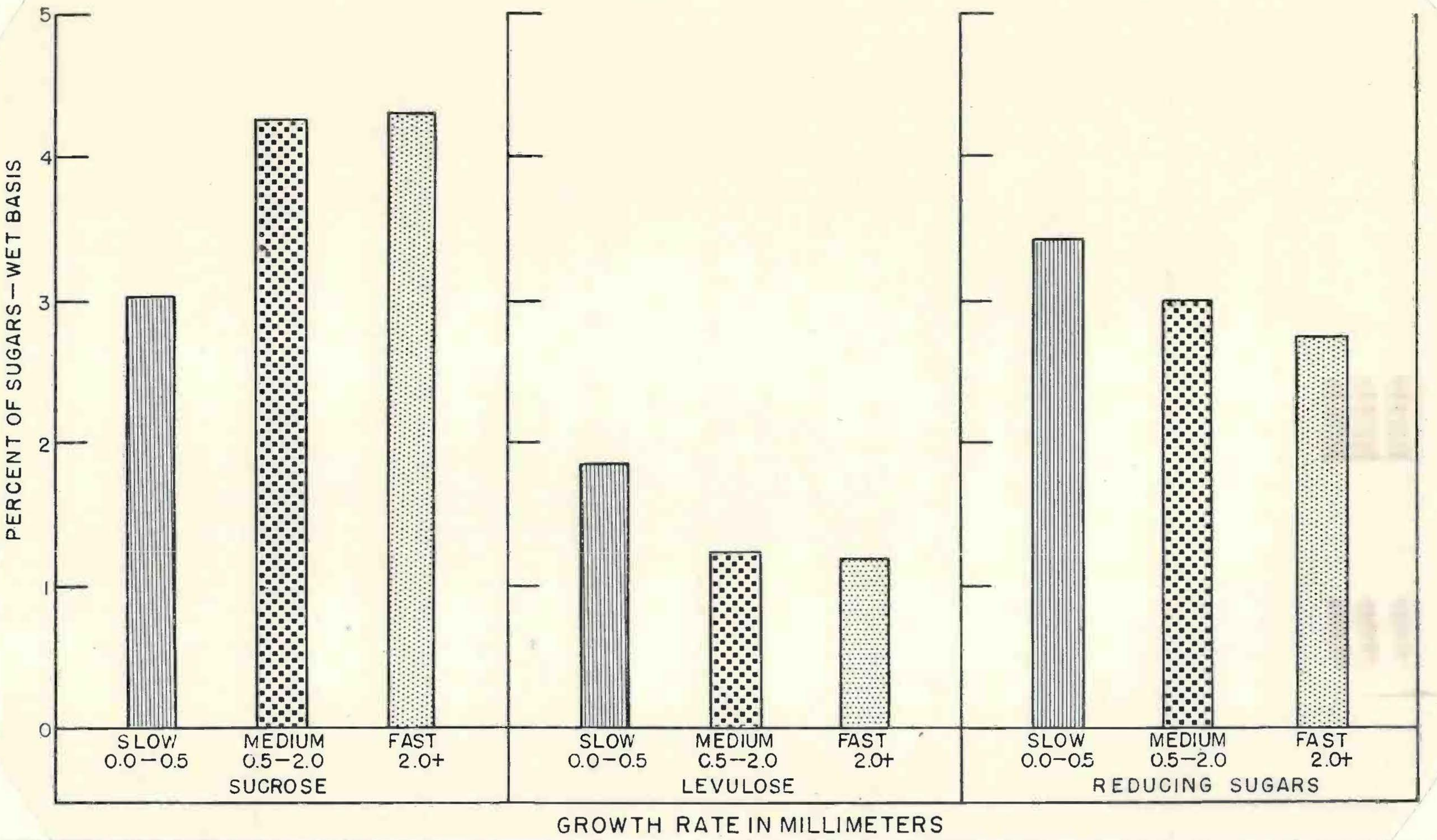

Figure 11 .- Relation between growth rate and the concentration of certain sugars in the living bark of ponderosa pine.

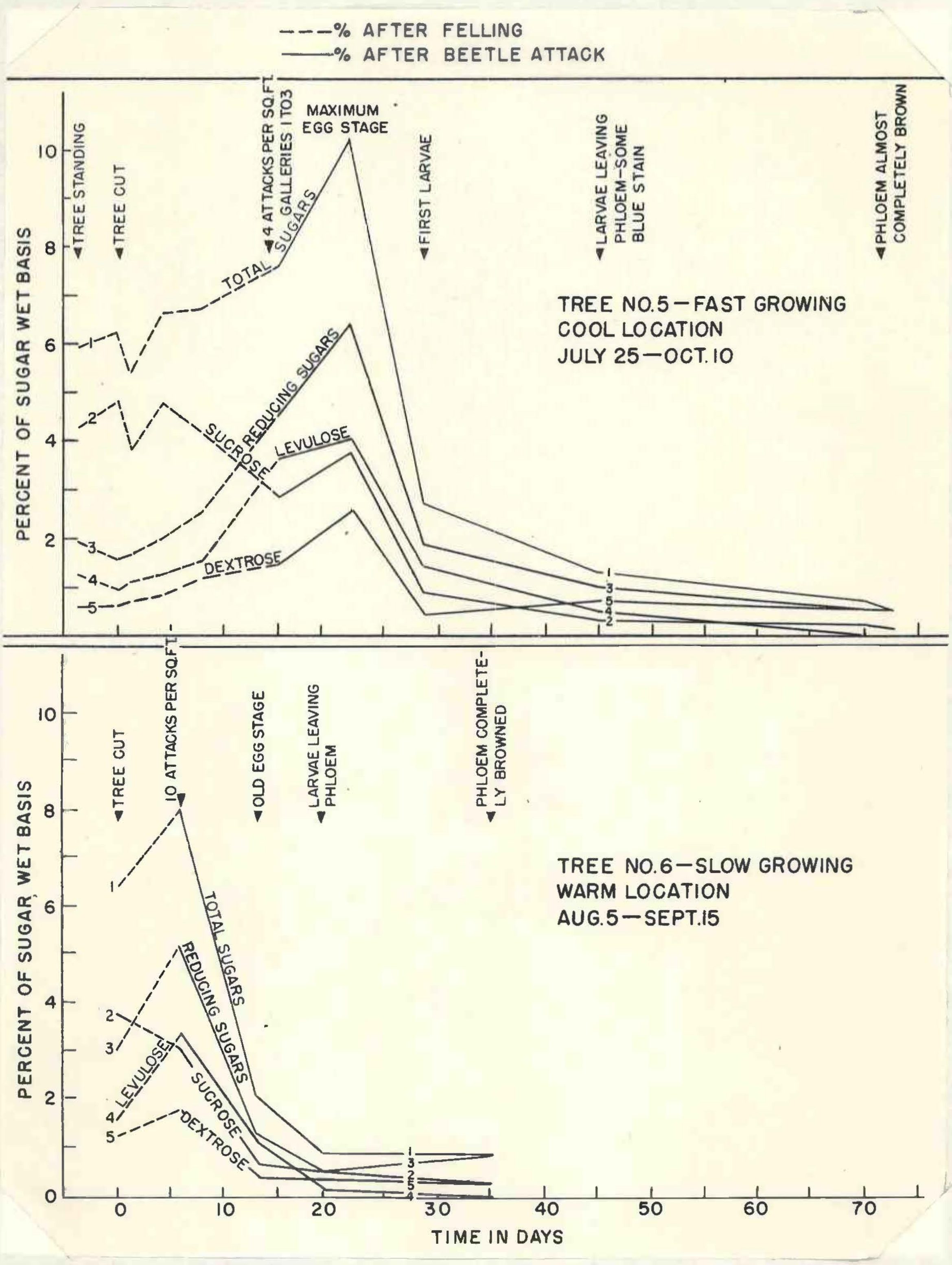

Figure 12.-Changes in concentration of certain sugars in the living bark of ponderosa pine following felling and western pine beetle attack.

"In spite of the small amount of data, the results indicated:

1. A pH below normal at the time of attack on trap logs.
2. A tendency for trees to approach this attractive pH during the season following injury.
3. An increase in pH shortly following attack and during the development of broods.
4. No relation between rate of growth and the pH of the inner bark.
5. A change in trap logs away from the normal and toward the acid side of the range."

The results of all of these attraction studies were summed up by Person (U236) in his final report on the project. These were stated as tentative conclusions:

"1. The inner living bark is the most attractive major part of the tree; the outer bark ranks second, the sapwood third, and the needles are the least attractive of the parts of the tree that were tested.
2. No consistent difference was found in the attractiveness of slow and fast growing trees, as a whole, after being felled.
3. The attractiveness of a tree increases almost immediately after being felled. The degree of attraction apparently increases for a few days and then decreases,
4. Fermenting inner bark, if comparatively fresh, is the most attractive of the substances tested.
5. Turpentine and bark oils distilled from western yellow pine are apparently neither attractive nor strongly repellent. Mirov found that some of these oils were much more repellent than others, and that the lower the boiling point, the less attractive the oil."

Olfactometer Experiments, 1933

In 1933, Gordon (36, U71) attempted to study the chemotropic responses of the beetle by means of a specially designed olfactometer. (Figure 13). By means of this apparatus, he tested a wide variety of chemical materials, with results that can be accepted only so far as the olfactometer gives a reliable measure of the responses of the beetle. Most of the chemicals tested were found to be repellent, and the pyridine and pyrrole derivatives were found to be highly repellent to D. brevicomis. However, two terpenes, linalool and laevo-menthyl acetate, were found to be slightly attractive. The most positive result secured by Gordon was the attraction to freshly fermented phloem of ponderosa pine. He found the phloem to be repellent for the first two days, but it became attractive after the third day. It became highly attractive on the seventh day, after which the attraction declined and at the end of 20 days of fermentation, it was highly repellent. This work of Gordon's confirms the results of Mirov's attraction experiments with fermented phloem. Gordon, however, continued the fermentation until it began to break down into acetic acid, which seems to explain the highly repellent results which he obtained after 20 days.

Figure 13 .-- Olfactometer designed by A. Gordon for testing chemotropic responses of the western pine beetle.

Gordon (36) concluded that (1) felled trees are always attractive, (2) some standing trees of a given species are more insect resistant than others, and (3) an initial attack may increase in intensity, presumably because of a stimulation by the production of attractive substances.

(Page 111a follows)

Figure 13 .- Olfactometer designed by A. Gordon for testing chemotropic responses of the western pine beetle.

BEPQ #8542

Person's Tree Selection Theory

Although the various studies that were made of attraction habits of the western pine beetle did not find an application in direct methods of control as was hoped, the results were highly suggestive and led to the formation of a theory which explains why the beetle selects certain trees. This theory has at least served as a background for the studies that were made later on the characters of susceptible trees. In a published article by Person (105), the explanation of what attracts the beetles to certain trees was stated as follows:

> "The initial attraction of beetles to a tree is due to the formation and escape of volatile aldehydes or esters, which are a by-product of a respiratory fermentation resulting from abnormal enzyme activity in subnormal trees. The causes of this subnormal condition may be drought, injuries of various kinds, or something else that interferes with the normal physiology of the tree.
>
> "This initial attraction, particularly in trees only slightly subnormal, is probably so weak as to be detected only by beetles in the immediate vicinity of the tree. After a few attacks are made, a second stronger attraction is started by the yeast introduced by the attacking beetles, and finding the inner bark a favorable medium for its growth. This secondary attraction is probably strong enough to attract beetles for a considerable distance with the result that the tree is usually heavily attacked and killed."

Although absolute proof is yet to be found for this theory, it is the most logical explanation that has yet been advanced for attraction of beetles to susceptible or high risk trees. However, in the actual practice of sanitation-salvage logging, which has since come into use, the selection of high risk trees is based on recognition of visual crown characters, and not of odors emanating from the trees. Until some means can be devised for detecting the esters to which the beetles respond, Person's theory of tree selection will continue to be a purely theoretical explanation of attraction.

In 1951, Callaham (U48) designed and built a wind tunnel at Placerville, California, to study the olfactory and air current tropisms of the western pine beetle. He was unable to find any significant beetle attraction or repulsion which could be attributed to fermented phloem or the oleoresins used in his tests, but did not feel that his tests were conclusive because of many factors which could not be readily controlled.

PREFLIGHT HABITS

What beetles do immediately after emerging from the bark is of particular interest when considering the possibility of killing them by contact sprays before they take flight.

Evenden (U57) was the first to describe an emergence which he witnessed near Coeur d'Alene, Idaho, in 1916:

> "Contrary to my expectations, the beetles do not remain upon the outside of the host plant for any length of time. This may be due to the fact that the day on which this record was taken was very warm. Upon emerging from the bark, the beetles rest for a few seconds, 5 minutes being the maximum length of time; then after raising their elytra for a few times and apparently testing their wings, they took flight in different directions. Many of them returned to the host tree for a few minutes."

Person (U229) also carefully recorded his observations of the beetles' preflight habits as noted at Cascadel on the Sierra National Forest in 1926:

> "The newly emerged beetles usually crawled about in search of an exposed point before attempting flight. They then spread and folded their wings a number of times and then took off. In many cases the attempt failed and the beetle fell to the ground, crawled back to an exposed point of bark and tried again."

Moore (U204) reported on the behavior of five western pine beetles which emerged from logs that were kept under close observation for 13½ hours. He found that the minimum length of time that all adults would be in contact with the log was 60 seconds.

FLIGHT HABITS

Once the beetle has found its way through the outer bark to the surface, it has the option of using two methods of locomotion - either crawling about on the surface or spreading its wings and taking flight into the air. Observations have shown that within a few minutes after emergence, it chooses the latter course. An adult is a very small dark object, and flies with a swift, irregular, darting movement. So it cannot be followed long by the human eye and no observer has been able to follow an individual beetle in flight any farther than about 100 feet from the brood tree. They have been seen only just as they are leaving the brood tree or when coming in to make their attack, and, as a result, we know little about the beetle as it flies about in the air spaces of the forest in search of new trees to attack. Just what it does during the greater part of the flight is a mystery that has intrigued many observers for many years.

Field Observations of Flight Behavior

At Ashland, Oregon, in 1916, Keen (U127) carried on a long series of observations and experiments dealing with flight habits. He studied the first reactions of the adults after taking flight by rearing beetles in large number in an insectary, liberating them in the forest at a fixed point, and then observing the direction in which they started to fly. At each point of the compass, he set up tanglefoot screens at a distance of 25 feet from the liberation point. These consisted of frames of window glass, 2 feet by 3 feet, on which tanglefoot solution was smeared. His results show:

> "They invariably followed the direction of the wind. After leaving the liberation board, they generally circled somewhat to gain elevation. If the breeze was at a lull, they would rise to a considerable height, 25-30 feet, and then caught by the breeze would be carried away by it. Beetles could only be followed by the eye for a distance not greater than 100 feet. Hundreds of beetles when liberated were observed to fly towards the frames, and then rise and fly over or around them, showing that they do not fly blindly into such an obstacle."

Person (U229) made observations on flight at Cascadel in 1926. He stated:

> "When successful [in taking flight], beetles flew off in a north or northeast direction, in the cases observed, at an angle between the horizontal and the perpendicular. The flight could be observed for a distance up to 100 feet, and in every case the beetle flew past the nearby trees with no evident intention of attacking."

Effects of Air Temperatures on Flight Behavior

All of the experiments and observations that have been mentioned so far were carried on under temperatures that permitted normal activity of the adults. Miller (88) records the range of active temperatures for adults as from 45 to 95° F.

Person (U229) checked the flight behavior under varying air temperatures in the field.

> "The optimum temperature for the beetles was found to be between 70 and 85° F. Beetles moved about actively, but normally in the sun at temperatures up to 85°. Many of them made successful attempts to fly. Between 85 and 95° the beetles were abnormally active and inclined to avoid the full sunlight. Their movements were hurried and attempts at flight were usually unsuccessful. Temperatures over 95° were too hot for the beetles. They avoided the full sunlight and when exposed to it, they hurried wildly about and often lost their footing and rolled into a bark crevice. Attempts at flight were usually unsuccessful. One beetle that failed to get out of the sun soon enough became dormant and died in about 3 minutes at 102° F.
>
> "These temperatures were taken on the bark surface where the beetles were found, with a corrected Eastman thermometer. Since the black beetles would absorb the heat rays of the sun, their internal temperatures would be considerably higher than temperatures at the surface of the bark."

Beal (U6) made a series of observations on the behavior of adult beetles under a fairly wide range of temperature and found that at 36° F. adults were capable of slow movements of the legs, but were unable to walk; at 48 to 50° they could walk slowly; above 50° activity increased with temperature; and adults were noted as "very active" at 84 to 88° F. Adults exposed to constant temperatures at 93 to 97° F. were "all dead at the end of 4 weeks," although they were kept in the natural phloem where they could feed.

These records indicate that the optimum temperature range under which adult beetles can sustain flight is between 70° and 85° F. When temperatures drop below 50° F., adults must cease flight and rest in some sheltered place. Temperatures above 95° are too hot for beetle activity in exposed places.

Influence of Weather Factors During the Flight Period

Weather conditions during the flight period introduce some factors which may limit or completely override any inclination which beetles may have to move in a given direction and may at times have a decisive effect upon the dissemination of the species. The weather factors which can be considered to have some effect upon the beetles during their flight period are wind, temperature, and unseasonable storms.

It has been shown that there is not sufficient evidence on the effects of wind movement to attach great importance to this factor in dissemination. The beetles are able to fly either with or against air movements of moderate velocity, so that they still have the option of response to other factors such as light or attractive host material. On the other hand, if numbers of beetles are caught in flight by winds of high velocity, it seems probable that they would be carried in the prevailing direction of the air movement. However, there is no evidence one way or the other on this point and no conclusions seem warranted, except that general dispersion of beetles throughout an area goes on regardless of wind and air movements.

Temperatures within the range of beetle activity are an essential requisite to flight. Sudden drops in air temperature to 50° or lower will arrest all flight movement until higher temperatures return. Therefore, a prolonged cold spell during the flight period can break the force of the attack that will be made within the affected area.

The weather conditions which most obviously interfere with the flight of beetles are those that come with unseasonable storms accompanied by precipitation and low temperatures. Late storms that come after emergence in the spring or early storms in the fall not only put a stop to flight movements of the beetles, but may result in a high mortality as well. One such case in the fall of 1932 was reported by Gustafson (U74) in connection with a control project on the Sierra National Forest.

> "The exceptionally late flight, ending December 11, 1932, was dissipated by the sudden cold weather and snow storm of December 12 to 17. This sudden drop in temperature, followed by a severe snow storm, caught many of the broods in full flight and they were consequently destroyed before they could secure protection by boring into the bark."

Furniss (U65) records a similar arresting of the emergence and flight of beetles in the Bass Lake area by cold weather in the late spring of 1934.

Still another possible influence upon dissemination for which evidence is lacking is the effect of dark, cloudy weather. All observations of beetles in flight in the field seem to have been made in bright, sunny weather. It is doubtful whether the beetles do much flying on dark days even though temperatures are favorable, since the light stimulus is greatly reduced. However, there is no evidence on this point one way or the other.

Swarming Habits

Webb (133) stated that the beetle "attacks living trees in swarms." He probably intended to convey the idea that they attack in great numbers because in all the years of subsequent western pine beetle investigations, we find no records that indicate any tendency on the part of the adults to move concertedly in masses, as do bees, termites, and grasshoppers. Flight is apparently an individual activity for each beetle. As they fly, they respond to certain stimuli and attractions, but these influences do not cause them to move in mass flights. Anything resembling true "swarming" in flight is yet to be recorded.

Duration of the Flight Period

The interval of time that elapses between the emergence of a beetle from its brood tree and its entrance into the bark of the tree that it attacks is obviously important to the survival of the insect. During this period the beetle does not feed, and it may be exposed to unfavorable weather and to predators. Its chances of meeting an untimely fate are multiplied as the flight period is extended. One would expect the beetle to attack as soon as possible in order to reach the shelter of the inner bark where it finds food and mate and where many of the factors unfavorable to its existence are excluded. But since it is quite impractical to follow the course of individual beetles, we have only indirect evidence as to how long they spend in flight.

Studies already described have revealed that the beetles do not all emerge at once, and that for the population as a whole there is a more or less continuous flight of beetles throughout the season. However, there are well defined peaks of emergence and then peaks of attack. It can be safely assumed that flight activities occupy much of the time interval between these two peaks. Keen (UL26) approached the question of the length of the flight period by comparing the peak periods of emergence and attack on the Lamb's Mine Unit in 1915 and 1916. He found that "from the plots showing quantity of emergence and quantity of attack on different dates, it would appear that maximum attack followed maximum emergence by 26 days."

Keen also found that caged beetles confined with a trap log "were capable of attacking 3 days after emergence." This has been confirmed by a number of subsequent caging experiments. However, it cannot be expected that beetles in confinement would follow the same behavior as beetles that have full freedom of flight in the forest. Under natural conditions the evidence all indicates that there is at least a period of a week or two following emergence during which the great majority of the beetles are either in flight or resting somewhere in the forest before they finally select and attack new trees. This period may be shortened or prolonged by weather conditions and season.

How Far Do Beetles Fly?

Webb (133) made the following observations:

> "After leaving the tree or trees in which they went through their transformations, the beetles fly away to find trees in which to deposit eggs. They may select a tree near at hand or may fly quite a long distance before making a selection."

This observation has not been changed materially by many subsequent studies of flight behavior. Webb, however, does not state how far is "quite a long distance," and this is the question that has absorbed most of the attention in flight studies. It is important because the distance that beetles may fly must be considered in setting the boundaries of control areas.

Keen (U127) first attempted to arrive at some conclusions as to flight distances by deductions from field data bearing on distances between infested trees of succeeding generations. He observed on the Lamb's Mine Unit that after the beetles emerged from an infested tree, a new tree would often be attacked soon afterwards in the general vicinity. On the basis of such records, he inferred that the beetles do not travel very far. "The distance of flight averages probably less than 100 yards." Other investigators and the spotters on early control projects arrived at the same impression by the simple process of noting the distances between recently abandoned and newly infested trees. Ralph Hopping in his survey work was fairly certain that the beetles attacked very close to the point of emergence.

This method of establishing flight distances by inference was admittedly inconclusive. The fact that a newly attacked tree is found relatively close to a recently abandoned one might merely indicate that the beetles in the surrounding area were being attracted to this particular site because they found here a supply of susceptible trees and favorable environment. In commenting on these first observations on flight habits, Dr. A.D. Hopkins stated in a letter:

> "There is no doubt that all of the Dendroctonus beetles can and do fly long distances from the trees in which they have bred, and that they are attracted to certain trees and centers from all directions. There is, therefore, no way of securing facts or evidence to prove where all the beetles come from that attack a tree near one from which the broods of a preceding generation have emerged."

Experiments with Marked Beetles

Keen (U127) planned and carried out an experiment in which he hoped to establish unquestionable records of the source of beetles coming to a newly attacked tree. To do this he proposed to mark a large number of beetles after emergence so that they could later be identified, liberate them from a fixed center, and then see if any of these marked beetles could be recovered from trees attacked near the liberation point.

The first obstacle in this experiment was to find a practicable technique for marking the beetles. After repeated experiments a suitable marking medium was developed consisting of rosalic acid dye dissolved in 95 percent alcohol. This was applied to the outer shell of the beetles in the form of a mist-like spray which dried very quickly. This application caused no apparent injury to the beetles and remained fixed even after the beetles had extended their egg galleries into the resins and water-saturated tissues of the inner bark of trap logs. Beetles so marked could be identified, even though they had received only a few drops of the solution by a color reaction when they were dropped into a testing solution of sodium hydroxide.

The liberation phase of this experiment was carried out in the spring of 1917. All of the infested bark was collected from 7 trees that made up all of the overwintering infestation on a mile square section of the Lamb's Mine Unit. The beetles from this infested bark were reared and allowed to emerge in an insectary; here they were marked and then liberated at a central point in the same section from which the bark was collected. A total of 8,000 marked beetles were liberated between June 15 and June 29.

No new attacks were found on this section until August 13 when a newly attacked tree was found about one-fourth of a mile from the liberation point. This was cut down and the parent adults collected from their egg galleries in the inner bark. They were preserved by drying. The experiment was interrupted by Keen's enlistment in the army and it was not until October that Miller (U171) tested the marked beetles and reported on the results. It was found that 181 out of 1400 attacking adults collected from this tree gave a slight reaction in the testing solution, indicating that they had been marked. The remaining 1219 beetles gave no reaction and had apparently come to the tree from some other source than the liberation point.

This experiment is the only attempt that has been made to trace marked beetles from the point where they took flight to the tree that they attacked. The results, insofar as they can be accepted, serve to confirm Hopkins' statement. While some of the marked beetles had traveled one-fourth of a mile to attack a new tree, they had been joined in this attack by many other beetles coming from some unknown source. What became of the remaining 7819 marked but unrecovered beetles which were known to have taken flight from the liberation point and how far they may have traveled before attacking is still an absorbing mystery.

Experiments to Determine Distance Beetles May Fly to Trap Trees

Patterson (U206) tried to obtain some positive records of flight distances by creating attraction centers in locations that were at fixed distances from any known sources where beetles were emerging. In one of these tests near Ashland, Oregon, he forced an attack on the base of a living tree by confining newly emerged adults in a cage enclosing the lower 8 feet of the trunk. Before the start of this attack, all infested trees within a radius of one-quarter mile of the caged tree were cut and the bark burned. Soon after attack started in the cage, beetles from outside sources attacked the entire trunk. These beetles were considered to have come from beyond the treated area, which would have necessitated a flight of at least one-quarter of a mile.

Trap trees, felled at isolated points during the flight season, have been used as another method of determining how far beetles may fly when attracted to some particular locality. Miller (U181) reported a record in 1918 of a trap tree located on the lower fringe of the Sequoia National Park which was successfully attacked. The nearest tree from which the beetles were considered to have emerged was 1.2 miles distant.

Patterson (U207) also used trap trees in an isolated grove of pines in the Rogue River Valley to obtain a record of long-distance flight. This grove, which contained no bark beetle infestation of any sort when the trap was felled, was surrounded by an area void of pine; The nearest known bark beetle infestation was two miles distant. The trap tree was felled on August 19, and by September 15 *Dendroctonus brevicomis* and associated insects were attacking the log and stump. These beetles had apparently made a flight of at least two miles to reach the trap.

Records of Minimum Flight Distances

While trap tree experiments have indicated that some of the beetles may fly as far as two miles, they do not prove that it is the habit of the general population to make flights of that range. It is equally important to know whether some of the emerging beetles make relatively short flights and attack trees near the point of emergence.

Miller and Person (U183) carried out a series of experiments near North Fork, California, from 1921 to 1923, which shed some light on minimum flight distances. They attempted to introduce the western pine beetle into an isolated grove of ponderosa pine located some 3 miles distant from the main pine type and about 1,000 feet lower in elevation. These trees, occupying a favorable stream bottom site and all making vigorous growth, covered about one acre and were surrounded by grass and brush lands. No trees in the grove had been attacked by bark beetles for many years, if at all.

Felling a trap tree in 1921 failed to attract beetles. Transplanting infested bark into the grove in April 1922 from which 22,590 beetles emerged, according to exit hole counts, also failed to cause attacks on the living trees, although 492 pitched-out attacks were found on one tree around which most of the infested bark had been piled. In August 1922, a similar planting of infested bark brought similar results. In April 1923, another attempt was made by transplanting infested bark to start an infestation in this grove. This time a trap tree was also cut. Out of 3,000 beetles which emerged from the bark, about 500 went to the trap tree and successfully attacked it. No living trees in the grove were attacked.

This series of experiments by Miller and Person, aside from demonstrating that the western pine beetle could not be artificially established in the fast growing trees on this low elevation site, also indicated that only a very small percent of the beetles attack in the vicinity of the point where they emerge even when suitable host material, such as a trap log, is available. The great majority of the emerging beetles apparently went away from there, even though their flight in this case carried them out into non-timbered territory where there were no pines to attract them.

In 1926 Person (U229) obtained some further data on the minimum distances which some beetles may fly, this time by building up an emergence center within the main pine belt of the Cascadel unit. The site selected was infestation free, but contained a number of trees of low vigor which were considered susceptible to attack. It was expected that the beetles would be less likely to leave the point of emergence if susceptible trees were available. Although one tree was successfully attacked on the site where the infested bark was piled, Person's conclusions as to flight habits were: "Only a very small percentage of the emerging beetles attacked the tree at which the bark was piled."

The experimental evidence accumulated thus far indicates that some of the beetles may fly only a few feet or yards from the point of emergence to attack and that others may fly as far as two miles. However, the results support the theory that there is a strong tendency on the part of the emerging beetles to move away from the vicinity of the trees in which they are reared; and that this tendency predominates over the availability of attractive food material, such as suceptible trees and traps.

Average Flight Distances in Population Movements

While the experiments described thus far shed some light upon the maximum and minimum distances that a few beetles may fly, they did little to determine the distances that may be covered by the movement of large populations. This question becomes important in control operations, because an area that has been cleaned of infestation will become re-infested much more quickly by the mass movement of beetle populations from adjoining infested areas than by long flights of a few beetles coming into the area. A series of experiments was carried out during the period from 1924 to 1934 which were designed to determine the average flight distance covered by large numbers of beetles.

The Forked Meadow Flight Study, 1924

In the San Joaquin project in 1924, Miller and Person (U190) studied the rate at which a small unit may become re-infested from outside sources after all of the infestation that could be detected within the unit had been treated. On the Forked Meadow Unit, a circular area of 3200 acres, roughly 1¼ mile in radius, forming a natural watershed, all infested trees were located and treated by continuous control work throughout the season. The area was surrounded by pine type and within a border zone one-half mile wide, the location and emergence period for all infested trees were recorded, so that the nearest source of possible infestation was established.

As the experiment progressed, it was found that new trees were attacked in the control area about as fast as the infested ones were treated; and that the infestation within the control unit actually increased during the season despite the control work. This was also true in the border zone where infested trees were left untreated. In general the season of 1924 was one of increasing infestations everywhere and the Forked Meadow Unit was no exception to this trend. After the distances between recently abandoned and newly attacked trees on the experimental area had been measured, it was concluded that "the average distance from trees attacked to the nearest tree from which beetles could have come was less than one-half mile and did not exceed one mile at the maximum."

The Oat Mountain Experiment, 1925

Since the Forked Meadow experiment was carried out in a non-isolated, circular area with a radius of about 1¼ mile, no long flights by the beetles were necessary to accomplish its re-infestation. In 1925 Miller (U192) again tried a similar test under conditions requiring longer flight distances. This time he selected a peninsula of pine type which extended about two miles from the main pine type of the Cascadel Unit. Known as the Oat Mountain area, it contained about 2,500 acres. On three sides (southeast, southwest, and northwest), the pine type is bordered by brush and grass areas extending for a number of miles. It was assumed, therefore, that the beetles coming to re-infest the Oat Mountain area after it had been thoroughly cleaned of infestation could come from one direction only, northeast.

All of the 1924 overwintering infestation that could be detected on the Oat Mountain area was treated in the winter and spring of 1925. This operation left a clean area for the beetles to invade when the flight period opened in 1925. All trees within a mile of the control area from which the beetles emerged were mapped and the control area was cruised several times during the season to locate the new attacks. By the end of the season, the beetles had spread over the Oat Mountain area so that the distribution of the infested trees corresponded fairly closely to that preceding control. It was concluded that: "This spread represents a flight of one and one-half miles at the minimum and two miles at the maximum." The assumption that the beetles made long distance flights was supported by the fact that a group of three large trees was attacked at the extreme southern end of the type peninsula, indicating that: "The flight to these trees could not have been made by a few beetles attacking by mere chance, but must have been controlled by a definite attraction which drew the beetles in large numbers for a considerable distance."

The Devil's Garden Flight Study, 1928-1933

The results of both the Forked Meadow and Oat Mountain studies were not conclusive because the experimental areas were not completely isolated by type barriers. Although it could be claimed that the beetles had traveled distances of from one up to two miles to reach certain trees, there was no assurance that they did not start their actual flight from trees much farther away in the untreated adjoining areas. These results led to the conclusion that a true understanding of flight habits and distances could be arrived at only by conducting experiments in a completely isolated area, separated on all sides from other infested areas by wide breaks in the pine type.

One of the objectives of the Devil's Garden Extermination Experiment was to obtain data on flight distances under conditions of extreme isolation. (See p. 277). Timbered Mountain, on the Devil's Garden plateau, where the complete eradication of the western pine beetle was attempted, is separated from the nearest large area of pine type by a distance of approximately six miles. (Figure 14). There were, however, a few widely scattered pine trees in the intervening juniper type, but no beetle infestation could be found in these isolated trees.

Figure 14.—Devil's Garden Experimental Area, Modoc National Forest, California.

(Page 134a follows)

The objectives of the Devil's Garden Experiment were originally defined by Keen (U139):

> "1. To stop beetle loss on this unit.
>
> 2. To determine the reduction due to control from 1, 2, and 3 successive treatments of an infestation uninfluenced by adjacent infested areas. This would take into account the reduction or increase due to natural causes by comparing the trend of this infestation with the nearest untreated areas.
>
> 3. After 2 seasons of control carried out as in commercial operations where the removal of 100 percent of the infestation is never realized, a third season of very intensive work would be undertaken to determine the possibility of complete extermination.
>
> 4. If extermination is secured, the area should be watched to determine in what manner an isolated area becomes re-infested. Will the beetles fly in quantities over a barren area of 6 miles, and if so are they able at once to kill standing trees, or must they first breed up in broken tops, windfalls, or other weakened material?
>
> 5. The area also lends itself to a complete study of the character of infestation present in every tree and a determination as to what extent trees may die without the agency of insects."

The history of the control experiment is given in the reports by Salman (U250) and is summarized by P.C. Johnson (U116). While the *D. brevicomis* infestation in the extermination area was greatly reduced during the control period from 1929-1932, the beetle was still present in the area in sufficient volume to be an important factor at the close of the 1932 season. Losses were still continuing in 1933, but by that time the pine flathead, *Melanophila californica*, had assumed the major role in the death of the trees.

In summarizing data on the flight phase of this study, Johnson found that most of the new attacks during the control period were concentrated in the center of Timbered Mountain and towards its southern, southwestern, and southeastern boundaries. In these directions the nearest areas of pine type were from 12 to 30 miles distant. On the northern part of the area which was nearest to other bodies of pine timber and separated by a gap of only six miles, practically no new trees were attacked. Johnson concluded, therefore, that: "There is no evidence of beetles flying into the extermination area from surrounding pine stands several miles away. The continued bark beetle activity on the extermination area has come from within the area itself." Salman (U250) in a final review of the experiment gave the following brief summary: "Extermination of the western pine beetle was not secured. Flathead re-infestation may have come from within the area. Western pine beetle re-infestation, at least to a large extent, probably came from without the area. Control during 1929, 1930, 1931 and 1932 apparently did not reduce the losses markedly."

The Devil's Garden Extermination experiment was the last of the attempts of the Forest Insect Division to determine the flight distances of D. brevicomis by experimental methods. Like the experiments that preceded it, this one failed to yield conclusive results. However, the study did serve to emphasize the important role of associated insects and lends support to the assumption that their flight behavior is closely tied up with that of the western pine beetle. It is fairly obvious from the results of the composition studies that D. brevicomis can maintain limited populations in small bark areas of trees infested with flatheads or other associated species without being detected. If this is the case, then complete eradication is impossible unless all of the associated insects are also exterminated. The problem is further complicated by the presence of windfalls and injured trees which are difficult to find. It is doubtful if 100 percent eradication of the western pine beetle was accomplished in any of the experiments that have been described and the deductions concerning flight distances were largely predicated on the success of eradication on the experimental areas.

Observations of Migrations and Population Movements

As a general rule, the locations of infested trees from one generation to the next suggest that there is a certain amount of population movement from place to place within an infested area, and also between adjacent areas. One year a tree or group of trees is selected and attacked on one 40-acre tract; later in the season or the next year a similar concentration and attack may occur on the same 40 acres, or on an adjoining 40 or as far as half a mile away. However, under these conditions there is no constant direction in which the beetles are moving,or fixed pattern in this shifting of population centers. The beetles appear to be just milling around in the infested areas.

At times, however, what appears to have been mass movement of western pine beetle populations has been observed. These records indicate that the beetles traveled in numbers for fairly long distances and that there was a fixed direction to the course of the flights. Such movements have been observed but rarely and under conditions where great centers of population have built up to the point where favorable host material was becoming exhausted.

In 1922 Miller (86) found that new centers of western pine beetle attack suddenly appeared in areas where there had previously been little infestation following the build up of heavy populations in wind-thrown material. He reported that: "Although the heaviest killings were found close to the largest bodies of wind-thrown trees, groups of beetle-killed trees were found at points from 6 to 8 miles distant from any mass of windfalls. Apparently this was the result of a flight of part of the beetles emerging from the down logs."

Aside from conditions associated with windfalls, the sudden appearance of large groups of newly attacked trees in areas where previous infestation had been negligible has been observed during periods of epidemics. One unreported case is that of the Fence Meadow epidemic on the Sierra National Forest. Here an epidemic killed a high percent of the pine in the marginal sites of Blue Canyon from 1929 to 1931; the infestation in this area declined in 1932, but late in the summer of that year large groups of ponderosa pine were attacked in the adjoining Fence Meadow area at distances of two to four miles from the Blue Canyon infestation and on good sites from 1000 to 2000 feet higher in elevation. Since there had previously been no noticeable infestation where these new attacks occurred, the shifting of epidemic centers gave the impression of a mass movement of beetle populations.

Another case was reported by Gustafson (U73), in which he attributed losses in the reserve stand of the Sugar Pine Sale area on the Sierra National Forest to the migration of beetles coming from heavy infestation centers several miles distant. "The 1931 summer infestation was characterized by a tendency on the part of the beetles to leave the lower yellow pine belt, where the preceding winter attacks had localized, and strike in Site I and II conditions at the higher elevations. This apparent migration invaded the sale area, causing the loss of many seed trees left after cutting."

The evidence thus far available is not conclusive, but it suggests that the western pine beetle may make occasional migrations in numbers for long distances; also that this occurs only under exceptional conditions where large populations have developed to the point of overcrowding.

Summary of Information on Flight Behavior

1. At the beginning of their flight period, western pine beetle adults are positively phototropic to the extent that they will move toward lighted and away from darkened areas. However, the source of light appears to be only one of a number of factors that determine their direction of flight in the forest.

2. The beetles have been observed in flight only during the daylight hours. There are no records of beetles coming to artificial lights at night in forest areas.

3. Optimum temperatures for flight activity appear to be between 70 and 85° F. The beetles do not maintain flight when temperatures approach 50° F. and below, nor when they are above 95° F.

4. The beetles have not been observed to fly in swarms; i.e., large numbers of beetles moving en masse.

5. The beetles have been observed to move both with and against air currents. The extent to which wind movements may influence direction of flight has not been definitely determined.

6. Records of flight distances traveled to attack trees vary anywhere from the immediate vicinity of the emergence up to two miles or more.

7. There is some evidence that under special conditions populations may migrate for distances as great as six to eight miles.

8. On the whole, the original conclusion of Webb that "they may select trees close at hand or may fly for quite a long distance before making a selection" has not been modified by years of subsequent studies of flight habits.

THE SEASONAL GENERATIONS

Definitions

Hopkins (43) defined the term "brood" to mean "the progeny of a single pair (of beetles), or the individuals hatching from the eggs in a single egg gallery." The term "generation" he defined to mean all of the broods that are the offspring from eggs deposited at about the same time. True biological generations would be all the progeny of the same genealogical rank, but these are impossible to follow in the field, as parent adults lay some eggs in the fall, and then, after overwintering, may lay a second or third set of eggs in one or more trees in the spring.

Hopkins recognized the difficulty of distinguishing generations although he does not mention the complication due to the re-emergence of parent adults.

> "All the progeny of the overwintered broods may be said to comprise a complete generation. If all of this progeny complete their development between the time the first eggs are deposited in the spring and the close of the same season of activity, and emerge from the trees, it may be referred to as constituting a complete seasonal generation. If another set of broods develops to maturity from eggs deposited by the adults of the first generation of the season, it will form a complete second generation, and so on. If, however, only parts of the broods complete their development and emerge during the first season, and the others remain over until the next season, it will be a partial development of a seasonal generation. If all of the broods develop and emerge within twelve months from the time the first eggs were deposited, it is referred to as a complete annual generation."

Field workers, attempting to follow Hopkins' definitions, have found it most convenient to separate the seasonal generations by trees rather than by true biological generations. The first trees which are attacked in the spring by the emerging overwintering broods are known as first generation trees. When adults develop and emerge from these first generation trees, the new trees which they attack are known as second generation trees. If broods develop and emerge from second generation trees and attack before winter, these are the third generation trees, and so on. For the trees attacked by the main emergence of adults developing from advanced overwintering larvae, this classification corresponds to the true generations because the broods all pupate and the beetles emerge at about the same time owing to the temperature bar to prepupal development. But the classification of trees according to generations becomes very complicated as the season advances. Trees of the second generation may be attacked by new adults emerging from first generation trees, by late adults emerging from overwintering trees, and by re-emerging parent adults. By the close of the season these overlapping broods, together with differences in rate of development due to temperature, exposures, sites, and elevations, make the recognition of trees according to true generations practically impossible. This has led to a simplification in the terms used to designate the trees by seasonal generations, which has come into general use by those who conduct surveys and measure annual losses. The trees killed each year are separated only as overwintering trees, in which broods carry through the winter, and as summer generation trees, which are attacked and abandoned by the beetles within the season of activity.

Significance of Generations

Recognition of generations is of importance in determining the time of year that control work can be undertaken with assurance of finding all the broods in the host trees.

The number of generations which can be produced in a single season should be of importance in determining the potential destruction which the beetle can bring about. At least in theory, two generations annually should kill twice as much timber as one generation. However, studies have shown that the number of seasonal generations varies little under the climatic differences found within the range of the beetle's distribution, and that the degree of loss sustained in any particular region seems to have little direct relation to the number of generations produced annually.

Factors Affecting the Number of Seasonal Generations

The fairly consistent response in rate of development to temperatures as shown by studies already described would indicate that the number of generations produced in a season could be easily determined by summation of the cumulative hour-degree temperatures above the zero of development for any given locality. But those who have worked on the temperature requirements have found that it is not as simple as that. Whiteside (U321), after carrying through a long series of experiments with the development of mature larvae to callow adults concluded: "There appears to be no temperature which may be called the zero of development that will cover all stages of the western pine beetle at different seasons of the year."

In his discussion of the general seasonal history of the genus *Dendroctonus*, Hopkins (42,p.19) makes allowance for the modification of seasonal development by latitude and altitude, in accordance with his bioclimatic law:

> "In the spring of a given year, the average difference in the time of beginning activity, emergence, flight, etc. at the same altitude will not vary much from 4 days later for each degree north, or 4 days earlier for each degree south; while at the same latitude there will be a difference of about 4 days for each 400 feet of elevation in altitude.-- In the fall of the year the beginning of hibernation and other events will be earlier northward and later southward at localities of the same elevation; or earlier at higher altitudes and later at lower altitudes in the same latitude.
>
> "Of course there are exceptions to these rules in regions like that of California where remarkably abnormal conditions as to the influence of latitude prevail; and also in case of southern and northern exposures, sandy dry soils and wet clayey soils or bogs."

Seasonal Generations by Sub-Regions

So far records from infested trees have provided the basis for determining the number of seasonal generations that develop in any particular locality or sub-region. We find that records have been taken and interpreted from a number of localities which represent fairly well the climatic and other variables that affect development of the beetle throughout most of its geographical distribution. It can be assumed from these studies only that the seasonal generations which were recognized represent the individual interpretation of each observer. The date of emergence of overwintered adults, the first attack in the spring, the rate of development in these first attacked trees, the subsequent emergence, attack, and development on successive groups of trees are the principal events which determine the number of generations in the different localities studied.

Princeton, British Columbia

Lat. 49½ N., Long. 120½ W., elevation 1200-2500 feet.

Swaine (123) studied an outbreak of the western pine beetle in this northern limit of the ponderosa pine belt, and reported "one brood and a partial second each season."

> "The overwintered parent adults extend their tunnels, or start new ones, when the weather becomes warm in the spring, and deposit eggs. The adults developed from these eggs appear, apparently, early in August and start tunnels in the trees already attacked by the broods of overwintered young adults.
>
> "The overwintered young adults emerge from the red-tops during July and attack green timber about the old red-tops or spread to isolated trees or clumps.--- The larvae of this brood pupated and had in most cases left the bark as adults before the end of September. These adults apparently started fresh tunnels in the same trees, and deposited eggs, the larvae from which are to be found in the bark during winter.
>
> "The over-wintered larvae complete their transformations, emerge from the bark as adults, from the middle of July onwards, and start their egg-tunnels, probably at once, in the trees already infested.
>
> "The exact time of emergence of the different over-wintered broods will depend to some extent upon the altitude, location of the trees in regard to sunlight, and upon the lateness of the season."

Southern Idaho (Centerville area)

Lat. 44 N., Long. 116 W., elevation 3,000 feet

In 1905, Webb (133) studied the life history of the beetle in southern Idaho and recognized one and a partial second generation each season. The first seasonal generation attacked trees the latter part of June and emerged the latter part of August. Webb states: "The majority of (these) broods develop and emerge by the first of September, - but some pupae and young to matured adults may hibernate."

The partial second generation made its attack in late August and early September and these broods carried into the winter in the larval stage. "Eggs were found August 26 and as late as September.— It appears that the second generation — passes the winter in the larval stage and develops and emerges by the middle of the following June and first part of July."

By interpretation of the life history in southern Idaho, Webb forecast the number of seasonal generations to be expected in the warmer localities: "It is probable that --- in warmer localities of the Pacific Coast region, there would be two complete generations and possibly a partial third."

This surmise has been found to be approximately correct by subsequent studies.

East Central Oregon (Ochoco Area)

Lat. 44½ N., Long. 120½ W., elevation 3,500 to 5,000 feet

Buckhorn (U40) followed the seasonal generations in central Oregon during the seasons of 1932 to 1935 inclusive. He found considerable difficulty in separating the generations in the trees that were attacked. For example, in 1934 he found one set of trees attacked April 14-17 by re-emerging over-wintering parent adults and by the first emergence of overwintering new adults a month later (May 20). Then a second series of trees was attacked by adults from overwintering larvae. The emergence from these two series of first generation trees occurred the last half of July and throughout August.

The main seasonal generations recognized by Buckhorn in this locality included:

(1) First seasonal generation.-- Attack by this generation occurred through the latter part of May and extended to the first of July. The emergence from these trees occurred in late August and extended through September. In trees of this generation he found that "a few individuals remained in the bark to overwinter as mature or prepupal larvae."

(2) A partial second generation.-- Attacks of this generation occurred the latter part of August and through September. Buckhorn estimated that from 10 to 45 percent of this generation emerged from the south side of trees during September and October. The remainder overwintered as two-thirds to full grown larvae.

(3) A partial third generation.-- Attacks occurred in late September and October and brood from these went into the overwintering stage as eggs to half-grown larvae. Buckhorn considered that these third generation trees were attacked by a combination of late emerging adults from first generation trees, plus early emergence from second generation trees. The emergence of beetles developing from this generation, except for the re-emergence of parent adults in the early spring, did not occur until the following May and June.

Southern Oregon (Rogue River Area)

Lat. 42¼ N., Long. 123 W., elevation 3,000 to 4,000 feet

The life history of the beetle was studied intensively on the Lamb's Mine unit near Ashland by Keen (U126) in 1915 and 1916. He found that the attacks in some first generation trees occurred as early as March 4, 1916, as a result of emergence of overwintering new adults and re-emergence of parent adults; however, the peak of the attack by adults from overwintering larval broods did not reach a maximum until June 22. Emergence from these first generation trees occurred during the latter part of July and through August.

The attack of a partial second seasonal generation began on the first of August and reached its maximum September 6. A few new adults of this generation completed their development and emerged before winter; the remainder of the broods overwintered as full grown larvae and emerged the following spring.

A partial third generation developed from attacks occurring in September and October. Brood developing from these attacks overwintered as eggs and small larvae, and did not emerge as new adults until the following June.

In summing up the seasonal activity, Keen (U126) stated:

> "There are 3 periods of attack, 3 of egg laying, 3 of larvae hatching, 3 of pupation, 3 of beetles forming and 3 of emerging. These periods overlap to some extent, upon beginning and ending, but their points of maximum activity are easily distinguishable. Neither are they of equal magnitude. The overwintering generation is the largest generation; the first seasonal generation somewhat smaller, and the third partial generation very small indeed. -- There is in general one annual (seasonal) generation with a partial second and a partial third. At Ashland, Oregon, there is a maximum of 2 (complete) annual generations and a partial third, and a minimum of 1 annual generation."

Northeastern California (Modoc Area)

Latitude 41½ N., Longitude 121 W., elevation 5,000 feet

Studies were made near Hackamore, California, by Furniss (U65) during the 1933 season. He was able to distinguish the following seasonal generations for this locality. (Figure 15)

A first seasonal generation was established between the first of June and the first of August. Emergence occurred from the first of August to the middle of September.

A partial second seasonal generation was established from the first of August to the middle of October; a partial emergence began near the middle of November. By far the greater part of this generation overwintered in the large larval stage.

A partial third generation was established during October and the first part of November. The broods passed through the winter in the parent adult, egg, and very young larval stages, and were estimated to represent about 10 percent of the overwintering population.

Figure 15 .—1933 seasonal generations *Dendroctonus brevicomis* Lec., Hackamore, Modoc National Forest, California

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Southern Sierra Region (North Fork Area)

Latitude 37¼ N., Longitude 119½ W., elevation 3,000 to 4,000 feet

Seasonal history studies were carried on near North Fork, California, during the seasons of 1926 and 1927 by Person (U229); in 1932 by Furniss (U61), and in 1933 by Salman (U262). Although considerable variation was found between seasons and it is none too certain that all three workers were in entire agreement as to their interpretations of generations, their records show that there are at least three seasonal generations in this southern range of the beetle's distribution. (Figure 16). In general, the following seasonal generations were recognized.

Figure 16 .—Comparison of the 1932 and 1933 seasonal history of *Dendroctonus brevicomis* Lec. in the southern Sierra sub-region of California

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A first seasonal generation.—Attacks were recorded from April 25 to the latter part of May, the peak usually coming around the middle of May. Emergence from trees attacked by this generation began soon after the middle of June and extended to the first of August, with the peak of emergence occurring during the first half of July.

(Pages 151a,151b follow)

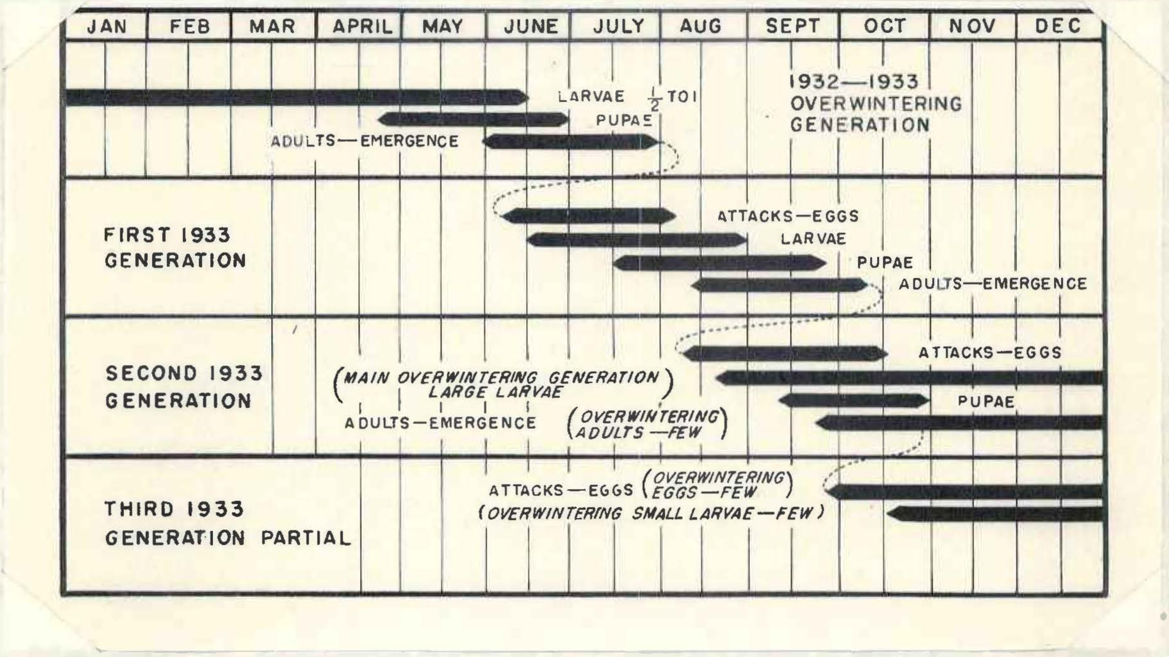

Figure 15.- 1933 Seasonal generations of *Dendroctonus brevicomis* Lec.
Hackamore, Modoc National Forest, California.

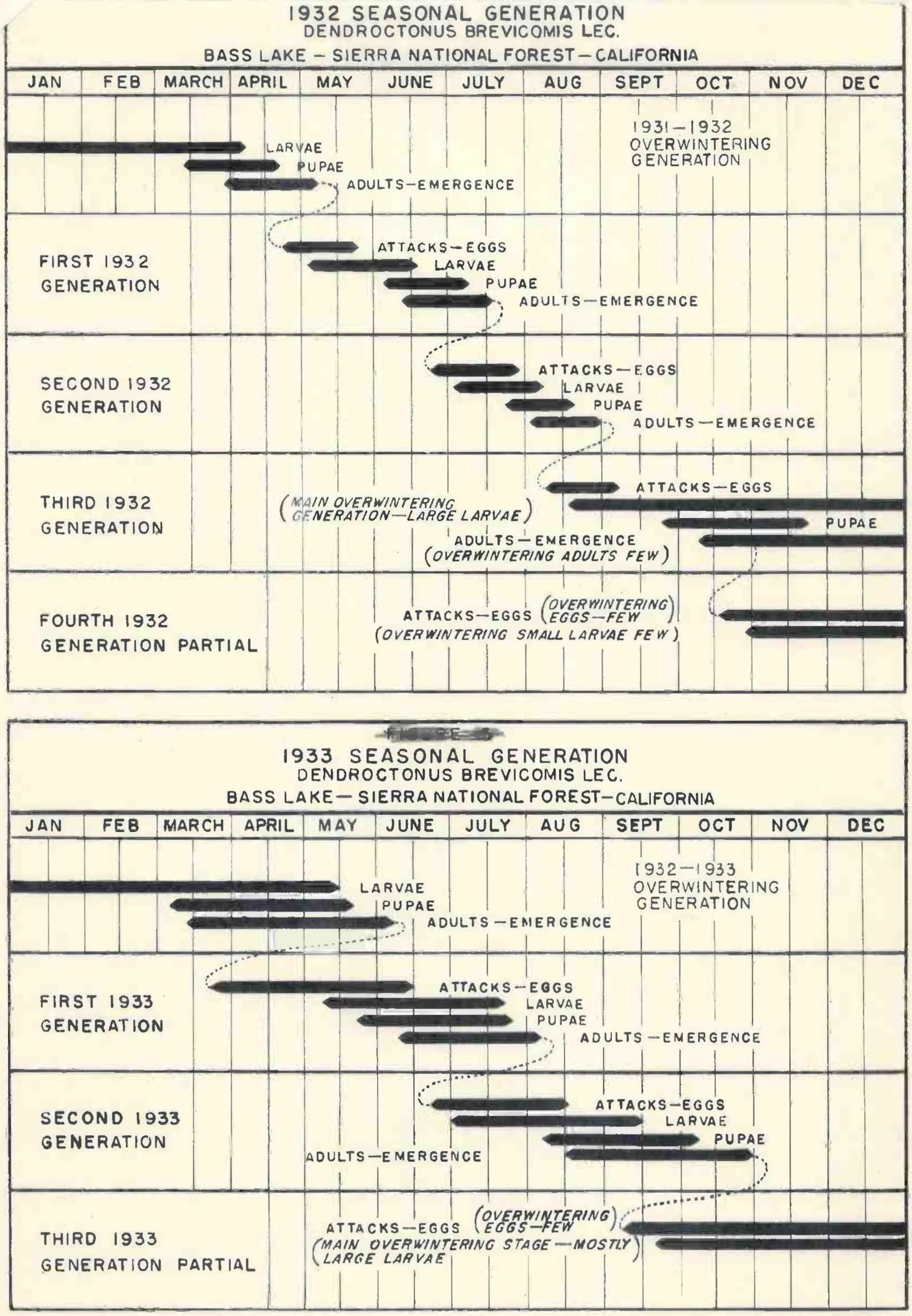

Figure 16 .- Comparison of the 1932 and 1933 seasonal history of *Dendroctonus brevicomis* Lec. in the southern Sierra sub-region of California.

A second seasonal generation.-- Attacks of this generation occurred from the last of June to the middle of August. Emergence began during the first half of August and extended to the end of September. The peak of emergence of this generation occurred during the first part of September.

A partial third seasonal generation.-- Attacks of this generation occurred from August 15 to November 1. In the main, this generation overwintered in the large larval stage. In the earliest of these third generation trees, the brood completed development and emerged during October and November. In those trees attacked late in the season, the broods went into the overwintering stage as parent adults, eggs, and small larvae.

A fourth seasonal generation was recognized by Furniss during the 1932 season and by Salman in 1934. The attack was established in the late fall (November) by a small portion of the third generation which emerged in October and November. This generation overwintered in the parent adult, egg, and very small larval stages.

Differences in Seasonal Generations

By Subregions

The differences by subregions can be accounted for largely by differences in latitude and longitude. According to Hopkins' bioclimatic law (page 403), there should be a difference of about 30 days in the occurrence of any given biological event between central Idaho and the southern Sierras at the same elevation. The observed events, just reported above, indicate a difference of about 60 days between the dates of attack of the first seasonal generation in the spring and nearly the same difference in close of activity in the fall. The British Columbia record indicates an even shorter season than in Idaho, while the central and southern Oregon and northern California conditions represent about the median of the range in time of given brood activities. Here the normal brood development takes place in one complete seasonal generation, a second partial generation, and a third partial generation each year.

By Elevation

The influence of elevation, according to Hopkins' bioclimatic law, is to retard development one day for each 100 foot rise in elevation. However, this rate seems to be nearly doubled in western mountain areas, and is greatly modified by such topographic features as slope and exposure.

In November 1915 workers at the Ashland, Oregon, station removed slabs of bark from a tree heavily infested with D. brevicomis and placed pieces, approximately two foot square each, on the north side of trees at a series of nearby altitude stations running from 2,700 to 5,700 feet. During the spring of 1916 these stations were visited at weekly intervals and emergence records taken.

Hopkins reported (44) the results of this experiment in the form of a table showing the departures from his bioclimatic law rates. (Table 1)

Table 1.--Effect of altitude on emergence of Dendroctonus brevicomis

Altitude	Departure from base station		
	Computed Constant Days	Actual Days	Actual from Constant Days
5,700	+ 25	+ 53	+ 28
5,200	+ 20	+ 36	+ 16
4,600	+ 14	+ 26	+ 12
4,200	+ 10	+ 19	+ 9
3,700	+ 5	+ 3	- 2
3,200 Base	0	0	0
2,700	- 5	- 17	- 12

Hopkins commented that this table "shows a striking example of departures from the constant caused by local influences."

In 1917 Miller attempted to determine the effect of elevation in the same locality and season by cage control on trap logs near Ashland, Oregon. He found that at the 2,000 foot elevation, two seasonal generations were completed between May 10 and October 15; while at the 5,000 foot elevation only a few miles distant, but one partial generation was completed between the same dates.

By Exposure

In connection with the altitude experiment report above, slabs of infested bark were placed on the north and south sides of the tree. As reported by Hopkins (44) there was a 20-day difference in the appearance of first pupae, 35 days' difference in transformation of first adults, and a 35-day difference in first emergence, with the warmer south side being earlier in every case.

By Seasons

Records show that there may be a marked difference between seasons in the rapidity of brood development, depending upon temperatures and length of growing season. (Figure 16). But at most this seasonal difference does not account for more than one extra partial generation. Evidence of this seasonal difference is shown by a series of records from the North Fork area in California. (U65, U262). Here the seasons of 1926 and 1933 were considered to have produced two complete seasonal generations and a partial third; while the seasons of 1932 and 1934 produced two complete seasonal generations, a partial third, and a partial fourth. Furniss attributed the difference to an early warm spring in 1932 and cold weather in the spring of 1933.

Effect of Reemerging Parent Adults on Generations

The re-emergence of parent adults and their extended period of egg laying in more than one tree does much to complicate the determination of number of generations and their exact beginning and ending. Attacks and egg laying by re-emerged parent adults often fill in the intervening gaps between attacks by new adults. During the season of 1934 (U262) the activities of the re-emerging parent adults were closely followed. They were considered to have produced two secondary generations (Figure 17) which overlapped the primary generations produced by the bulk of the broods.

Figure 17.-- Seasonal development of Dendroctonus brevicomis Lec., Modoc National Forest, season of 1934.

Summary of Information on Generations

(1) True biological generations of the western pine beetle are subject to so much overlapping and confusion as the season advances that they are impossible to follow. In survey practice, generations are arbitrarily separated according to the time that infested trees are attacked.

(Page 157a follows)

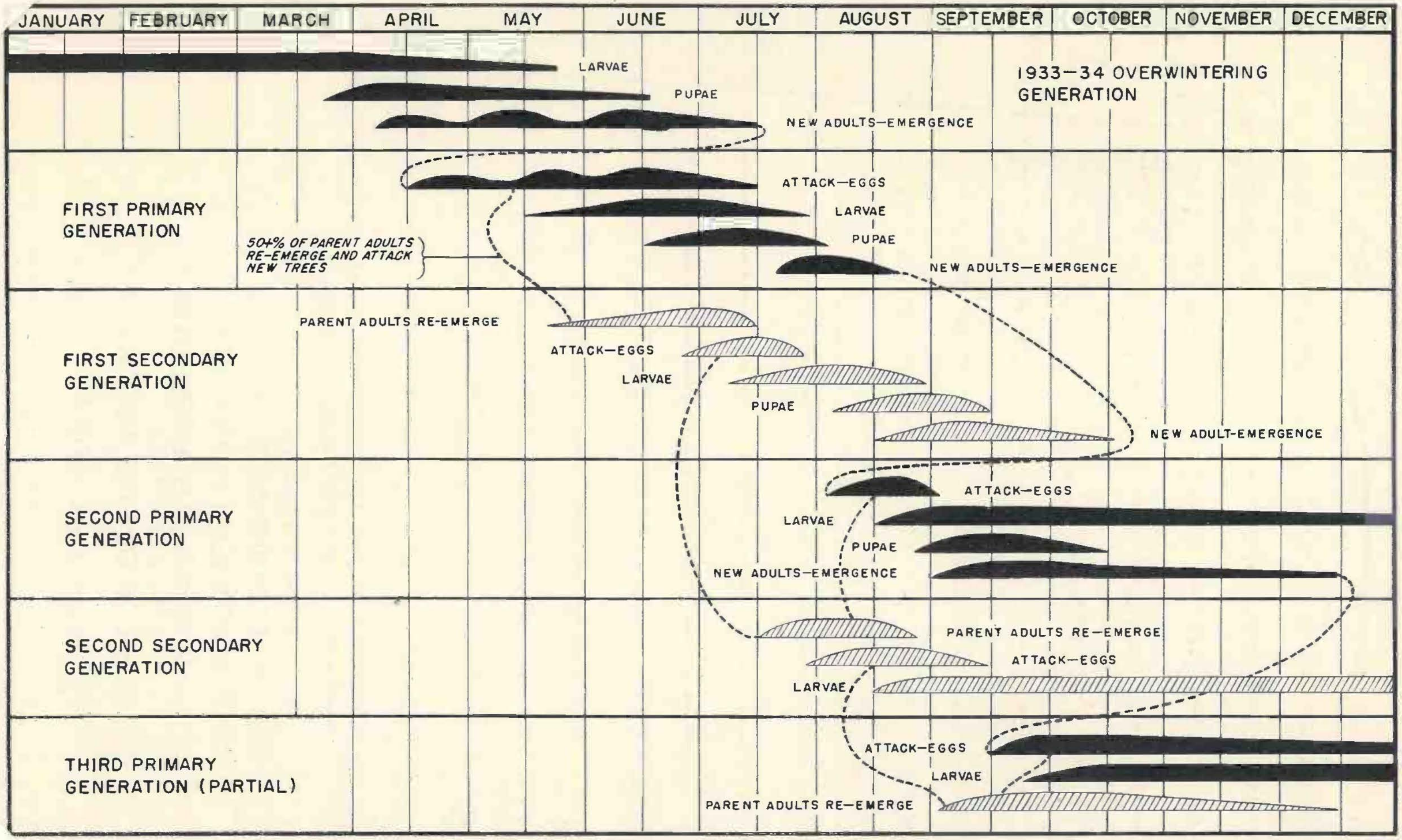

Figure 17.- Seasonal development of *Dendroctonus brevicomis* Lec. Season of 1934, Modoc National Forest, California.

(2) While the effect of temperatures and other climatic influences accelerate or retard development of the western pine beetle, the number of generations which are produced annually is limited in nature by the climatic extremes within which its principal host tree Pinus ponderosa is able to grow. This tree grows only where there is a definite winter period which produces not only a dormant condition in the growth of the tree, but in the broods of the beetle. Although we find wide extremes in the minimum winter temperatures under which ponderosa pine may grow, there are not great differences in maximum summer temperatures and in the length of season during which the beetles are active.

(3) It has been found that the number of seasonal generations differs between sub-regions and localities and between seasons in the same locality. On the average, each season, there are three distinct periods of attack, egg laying, and brood development, which, under the accepted definitions by Hopkins, go to make up one complete seasonal generation, a partial second, and a partial third seasonal generation. This average may be modified, by the climatic extremes that occur within the range of the beetle, to produce a minimum of one and a partial second generation to a maximum of two complete, with a partial third and fourth,generations.

SECTION III

BIOTIC RELATIONSHIPS OF THE WESTERN PINE BEETLE

THE BIOTIC POTENTIAL

Population Potential

Knowing the egg laying capacity of the western pine beetle, one might easily demonstrate by a few simple computations, that in a very short time its potential progeny could be quite overwhelming. With an average of 48 eggs per female and two generations a year, we could have from one pair of beetles 48 adults after the first generation, of which 26 would be females and 22 males; and 1,248 adults after the second generation, of which there would be 674 females and 574 males; and 32,352 adults after the third generation. With this rate of increase, the progeny would reach astronomical proportions after a few years.

If we disregard this potential increase and compare only the number of beetles that attack a tree with new adults which emerge, we find that on the average enough beetles are produced in one tree to attack and kill five more trees of the same dimensions; and these in turn should produce enough beetles to kill 25 trees; and by the third generation, we can expect a loss of 125 trees. This may not seem like a high rate of increase compared with the capacity of other insects, but, when the tenth generation is reached, which would require about four years, the progeny from the beetles produced in the first tree would be capable of killing 9,765,625 trees. As these increasing populations build up like an inverted pyramid, it would not require many years before enough beetles are produced to kill all the ponderosa forests in the west, except the very young trees which are immune to attack.

But we know that nothing of this sort ever happens. The long history of western pine beetle epidemics shows that population increases are inevitably followed by decreases. Somewhere in the complex environment of the beetle are factors that keep its numbers within limits far below its natural endowment for multiplication. These natural factors of control have been the subject of much speculation and study since the beginning of bark beetle investigations.

Hopkins (42) discussed the problem under the topic of "Favorable and Unfavorable Conditions of the Beetles." For Dendroctonus as a whole, he considered that climatic influences, temperatures, trees injured by lightning and fires, slash from storms and timber cutting, and trees affected by over-maturity and diseases are all environmental factors that operate in some cases for and in others against the increase of beetle populations. Among the direct enemies of the beetles, he mentioned predatory and parasitic insects, birds, and insect diseases. These first discussions of the beetle's ecology by Hopkins were too generalized to serve as a basis for recognition of specific conditions that forerun an increase or decrease of beetle populations.

Much work has been done since the publication of Hopkins' bulletin by various workers who have tried to take apart the complicated biotic relationships of the western pine beetle and to find out by analysis just what the controlling factors are and how and when they operate.

Population Statistics

✓ The first attempt to determine the number of beetles that make up the population of an infested tree was made by J.D. Riggs (U241) in 1913. He felled a tree 32 inches d.b.h. containing overwintering broods, cut up the bark, and counted all the beetles he could find in the inner and outer bark. He reported finding a total of 33,230 larvae and young adults. No one attempted to verify or dispute his figures.

On the basis of the brood statistics determined from all the bark counting done so far (see page 93), a fair estimate of the total population of an infested tree is as follows:

Average population for an infested tree

	Average per sq.ft.	Per av. tree *	Per M.B.F. volume
1. Number of parent adults attacking	25	8,625	10,450
2. Number of eggs	648	223,560	270,980
3. Number of larvae			
advanced larval period	188	64,860	78,618
prepupal period	122	42,090	51,018
4. New adults emerging	92	31,740	38,460

* Based on average tree of D.B.H. 25.2 inches, volume 825 board feet, bark surface 345 square feet.

(No text for page 163)

Normal Brood Mortality

As these average population statistics show, the potential increase in beetle population as determined by the egg laying capacity of the female is normally reduced in each stage of brood development so that from 11.6 attacks with 648 eggs laid per square foot by ~~28~~ 25 parent adults, only 92 beetles develop, or a reduction of 86 percent. Thus in nature only about one egg out of seven actually goes through all stages of development to become an adult and finally emerge. What happens to the other six eggs is a question that has been given considerable study without developing the full answer. Of those beetles that emerge, a great many are undoubtedly lost in flight and never manage to make a successful attack.

In addition to the average or what might be considered as normal mortality, broods are frequently hit by some catastrophe, such as extreme cold weather which produces abnormal or nearly complete mortality. Thus the vicissitudes of a beetle's existence and the many natural control factors operating to reduce its potential populations are what save forests from early and total extinction.

THE FACTORS CAUSING BROOD MORTALITY

During the Broods' Developmental Period in the Host Tree

During the long period of brood development in the bark of the host tree, the hazards of life are many, and at any stage from egg to adult mortality of progeny may occur from a variety of causes. The factors causing mortality that have been explored include unfavorable moisture, lethal temperatures, nutrition, competition for food supply, parasites, and predators.

Unfavorable Moisture Conditions

An excess of moisture or extreme dryness of the bark may be unfavorable to brood development and cause mortality.

Keen (U126) made the following observations on the effect of excessive moisture on the hatching of eggs.

> "No definite figures were obtained on the average percent of eggs hatching. However, it was noted that in some cases a good many eggs die or are killed in the egg niches. In some sour-sap trees, the entire brood may be killed by the moist condition. In other trees, which are normal, a varying percent fail to hatch."

Excessive moisture conditions in the inner bark appear to be quite detrimental to the first instar larvae. The high mortality of young larvae in the inner bark of sour-sap trees has been observed and noted.

occurs

Beal (U6) measured the moisture contents of logs and slash where high brood mortality was occurring and reported that:

> "excessive phloem moisture of 200 to 300 percent which invariably obtains in logs and slash kept within the temperature limits for brood development may be responsible either directly or indirectly for a large share of the brood mortality. We know that in standing trees where brood development of the western pine beetle proceeds normally, there is a rapid loss of moisture which accompanies good brood development."

Whiteside (U321) undertook to determine the amount of moisture in the outer bark which permitted satisfactory brood development. He determined the moisture content in 12 bark samples from infested trees with normal development and found that this averaged 12 percent on an oven-dry basis. This condition in the outer bark he found corresponded to a relative atmospheric humidity of 56 percent.

The actual correlation between the amount of bark moisture and larval mortality is yet to be determined on a quantitative basis. General observations indicate that excessive moisture conditions which produce high mortality occur at times in the field, but are limited to sour-sap trees, slash, and windfalls. The sour-sap conditions usually affect only the lower bole of standing infested trees, so that broods in the upper bole are not affected.

The amount of desiccation necessary to produce mortality in bark that becomes too dry has not been given attention. It would appear that in nature the storage of moisture in the sapwood of attacked trees and logs is passed on to the inner and outer bark in sufficient volume to provide for satisfactory brood development.

The Lethal Low Temperatures

Scope of investigative work.— The western pine beetle like all other forms of life cannot survive extremes of either high or low temperatures. It was found in the early western pine beetle studies that sub-zero weather which reaches lows of -15° to -20° F. usually results in some mortality among overwintering broods, and if such temperatures are prolonged for days or if the minimums fall much below -20°, the mortality may be high and current populations of the beetle will be greatly reduced. The interest in this phase of the insect's biology has been shown by the great amount of investigative work and the long list of publications and reports dealing with lethal low temperatures. Hopkins (42) referred to the effects of low temperatures only briefly.

> "While the severe cold at high elevations in which most of the western species prevail appears to have no detrimental effect on the overwintering broods, we have a striking example of its effect on a northern migration of a southern species in the complete extermination of the southern pine beetle in the Virginias by the exceptionally cold winter of 1902-03."

The first record of extensive killing of overwintering broods of the western pine beetle was made by A.J. Jaenicke of the Forest Service. In December 1924 minimum temperatures of -20° to -25° F. occurred on the Metolius area of Oregon, near Bend, where a control project was underway. (87). It was found that following this cold spell from 25 to 80 percent of the overwintering larval broods were dead in the bark. This discovery stimulated a long series of investigations and experiments to determine just what temperatures were fatal to the beetle.

The importance of low temperatures in the reduction of beetle populations was again emphasized by extreme cold spells which occurred during the winter of 1932-33 in Washington, Oregon, and northern California. The first cold wave of early December 1932 brought temperatures of from -20° to -38° F., throughout the entire range of the beetle in the eastside pine type, followed by a second cold spell in February 1933 which dropped temperatures to an all time low in Oregon of 54° F. below zero. These cold periods resulted in high beetle mortalities ranging from 50 to 90 percent of the overwintering broods. The average mortality throughout the eastside pine type of California and Oregon was estimated at 70 percent. The effects of this freeze upon the 1933 beetle population were closely studied through the funds and facilities made available by the CCC program of the Forest Service. (89,90,91).

Other periods of cold weather which resulted in some reduction of populations were recorded in November 1935, in January 1937, (U270) and in February 1939 (U317). For these cold spells, however, appreciable mortality was found only in local areas. So far no cold periods yet recorded have approached the historic cold wave of December 1932 in either the degree or the amount of population reduction.

The potentialities of cold weather in the natural control of the beetle were considered to warrant a program of intensive field and laboratory studies by the western forest insect laboratories which continued from 1933 until 1940. It is the results of this research program which have provided a fairly adequate basis for the interpretation of lethal temperatures in the natural control of the beetle.

Laboratory studies dealing with effects of low temperatures.—

Conditions of exposure and techniques.— In laboratory studies hundreds of tests have been carried out to determine what happens to the larvae when they are exposed to temperatures below the range in which they are able to maintain activity. Most of these studies have been concerned with temperatures below freezing. These experiments have used various methods of exposing broods to air temperatures in refrigeration apparatus. In some cases infested bark sections were exposed to the temperatures under study and results determined by shaving up the bark and recovering the larvae after exposure. In other experiments, entire blocks or small logs were exposed. In the greater number of tests, however, mature larvae in the outer bark were removed and exposed "naked" to cold air in the refrigeration compartments.

The technique that was most generally adopted for the western pine beetle after various trials with different media and procedures is that described in the report by Miller and Struble (U196). The larvae were first removed from the bark and placed in an individual paraffin cell. These cells were in blocks of fifty each and were open at the top so as to permit free access of air to the body of the larvae; at the same time the paraffin walls protected the larvae from each other and from the hazards of handling. An important requirement was found to be allowance for sufficient time of exposure at any given temperature for the body of the larvae to be chilled to that point. It was found that when the larvae were exposed to a gradual lowering of air temperatures at a rate of 4 or 5° per hour, the effects of any given temperature became apparent very soon after the point was reached. If larvae were transferred suddenly from warm active temperatures to an air temperature held at any fixed point below freezing, it required about two hours for the effects to register. In general, it was found that the containers that were used, whether the natural bark, (Figure 18) paraffin cells, or paper cells, made little different in the results as long as the body of the larva was chilled to the temperature under consideration. This factor is described by Yuill (U332, U334).

Figure 18.- Cells in ponderosa pine bark used in exposing larvae to critical low temperatures.

(Page 170a follows)

Figure 18 .- Cells in ponderosa pine bark used in exposing larvae to critical low temperatures.

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Terms used in defining the effects of temperatures.-- If a group of 100 western pine beetle larvae are all exposed under perfectly uniform conditions to the same range of air temperatures from 0 to -10° F., they will not all die at the same time or at the same temperature. For overwintering broods it has been found, on the average, that after the larvae have been chilled to a temperature of 0° F., the mortality will vary from 20 to 50 percent; at -2½° F., from 50 to 75 percent; at -5° F., from 75 to 100 percent; but at -7½° F., the mortality is practically always 100 percent. These differences in the amount of mortality, due to individual variations in cold resistance among any selected group of larvae at given temperatures, have made it necessary to adopt terms applying to these variations. The following were proposed by Miller and Struble (U196) and they have been generally used in subsequent studies.

Temperature points.-- The minimum temperature to which the body of the insect is chilled.

Freezing point.-- The temperature at which the body of the insect becomes frozen due to crystallization of the free water in the alimentary canal and body tissues; this condition does not necessarily result in death. This term was first used by Robinson (107).

Critical point.-- The temperature at which death occurs as a result of cold. The bound water crystallizes and the body cells are destroyed. This point may occur from 5 to 10° below the freezing point.

Critical range.— The range of temperatures from the highest point where slight mortality due to cold occurs to the lowest point where complete mortality occurs.

The *initial critical point* is the highest temperature in the critical range; the *ultimate critical point* is the temperature at which the mortality becomes complete; and the *intermediate critical points* apply to temperatures within the critical range.

Low temperatures that are critical to larvae.— These can best be discussed according to the effects that have been observed at different temperatures, proceeding from the higher to the lower temperatures in the range that have been studied.

50° F.— Larvae at this point and below become sluggish and dormant. "Failure of broods to develop at low temperatures below 50° F." (U6) indicates that metabolism ceases.

15 to 10° F.— Larvae may "freeze," but recover if brought back to warm temperatures. (88). This is apparently dependent on the amount of free water in the tissues. Yuill (U330) was unable to develop this condition by exposing larvae at 12° to 14° F. and stated that "in these tests, the larvae did not freeze until exposed to a temperature of 10° or less and the effects in practically every case were fatal." This contradiction calls for further investigation to clear it up.

10 to 7½° F.— The initial critical points for active summer brood larvae occur here. Yuill (U332) found mortalities around 50 percent at 7½°. For overwintering larvae no appreciable mortality due to cold occurred from prolonged exposure at 10° for 39 hours. (U196). Yuill secured low mortality (16 percent) of overwintered larvae after exposure of four days at 7½°.

7½ to 5° F.— These are highly critical points for active summer brood larvae. Yuill (U332) found 96 percent mortality for larvae of summer broods from the southern Sierra region, 60 percent from the Modoc region, after two hours exposure at 5°.

5 to 2½° F.— Few active summer brood larvae survive these temperatures after two hours' exposure. Yuill (U332,U333) found 100 percent mortality at 2½° for southern Sierra material, and 84 percent for Modoc material.

The initial critical points for the least hardy overwintering larvae occur within this range. Low mortality develops at 5°. Miller and Struble (U196) recorded 42 percent mortality after one hour of exposure at 2½°; mortality increased progressively with time of exposure up to 7 hours when it reached 76 percent.

2½ to 0° F.— These are important critical points in which the first effective mortality of overwintering larvae becomes apparent. In many laboratory tests that have been run with overwintering larvae, variable mortality has always developed in this range, usually from 20 to 50 percent. Miller and Struble (U196) compared overwintering broods from the Sierra, Modoc, Ochoco, and Coeur d'Alene areas, representing regional extremes in the range of the beetle, and found appreciable mortality at 2½° in all cases.

-2½° F.-- This point is near the middle of the critical range for overwintering larvae. Mortality is variable, depending upon degree of conditioning, but is usually in excess of 50 percent.

-5° F.-- High mortality of overwintering broods always occurs at this point. Two carefully checked tests by Yuill (U332) show mortalities of 96 and 100 percent with two hours' exposure.

-7½° F.-- Larvae die quickly at this point, the mortality usually reaching 100 percent with an exposure of one or two hours. (U332). Only two records are found of survival at this temperature by conditioned overwintering larvae. Miller and Struble (U196) exposed broods in bark sections from the Coeur d'Alene and Ochoco National Forests by gradually chilling the bark down to this point. The mortality in the Coeur d'Alene material was 81.9 percent and that in the Ochoco material 75.7 percent. In material from the Sierra National Forest the mortality under identical treatment was 100 percent. In larvae removed from the bark and exposed in paraffin cells, the mortality at -7½° was 100 percent from all regions.

-10° F.-- There is only one record of survival at this point in laboratory tests. Ten percent of the larvae in bark from Coeur d'Alene survived after temperatures had dropped to this point. This may have been due to variations in temperatures within the bark or irregularities in temperature control.

$-12\frac{1}{2}^{\circ}$F.— No larvae have survived exposure at this point in laboratory tests. However, in the field, using bulb thermometers under the bark, Beal (U11) found survival of 36 percent after bark temperatures had reached -14°F.; and at -17°F. the survival was 27.6 percent. This difference was thought to be due to one or a combination of factors; first, the difference may be due to variation between field and laboratory tests; second, temperatures in the field reached their low point for only a very brief period; third, it may be due to the fact that a previous freeze had already killed about 50 percent of the broods, and the remaining larvae may have been principally the hardier individuals; and fourth, broods from eastern Oregon are probably more cold resistant than those from the southern Sierras in California.

Cold hardiness of the larvae.-- In summarizing the work that was done on cold hardiness of the western pine beetle, Yuill (139) recognized a summer and winter condition of the larval broods. "Under the summer condition, the critical temperature range was 10° to -2½° F.; and under the winter condition, 5° to -7½° F." The term cold hardiness used to describe this increased resistance of the winter larvae has been used by Robinson and others in studies of other insects.

From tests of field material, Yuill found increased cold hardiness of the overwintering larval broods does not set in until late in the fall.

> "The critical range (10° to -2½° F.) remains at the same level with the beginning of cool weather late in October or early November, when within 6 weeks or less cold hardiness increases to the winter condition (0 to -7½°). -- It also appears that the level of resistance developed each winter is always the same whether the season is mild or severe."

The degree of cold hardiness developed by the western pine beetle was found to be far less than that of its near relative the mountain pine beetle in sugar pine. While the difference in the critical range between summer and winter conditions of the western pine beetle is approximately 5°, that of the mountain pine beetle was about 10°. In lodgepole pine of the northern Rocky Mountain region, the mountain pine has been found to develop resistance to temperatures of -25 and -30° F. according to Evenden (U58).

The cause of cold hardiness has been attributed to the ability of the larvae to change the fat and moisture content of their bodies so as to prevent the crystallization of bound water in the cells. Yuill (139) was able to induce a limited degree of cold hardiness by subjecting larvae for a long period to temperatures slightly above freezing. Larvae in the outer bark collected in November and stored at a temperature of 36° F. for a period of 35 days were able to withstand about 2½ more degrees of cold than when first collected. Mountain pine beetle larvae survived temperatures 10° lower after similar conditioning.

A start was made by Yuill (U334) in determining the changes in fat and moisture conditions that go with conditioning for cold hardiness with both the western pine and mountain pine beetles. The results were little more than indicative.

> "Although *D. brevicomis* larvae contained a much higher percentage of fats than do *D. monticolae* larvae, the iodine and saponification values were both lower than in the fat from the latter species. Such a fat would be less available under low temperatures and so might be a factor in limiting the development and resistance of this less hardy species."

Since studies along this line involved a complicated technique with results that could be expected to shed light only on the fundamental phases of cold hardiness, they were not continued after these preliminary tests.

The time factor in exposure to critical temperatures.-- As a rule the sub-zero temperatures to which overwintering larvae are exposed in the field are of relatively short duration, usually lasting no more than a few days at the most. Quite a number of laboratory tests were run to determine the importance of the time factor in increasing mortality. It was found under refrigeration control that for the lower critical temperatures, it required about 20 minutes' exposure for the first lethal effects of any given temperature to register. With two hours of exposure, however, most of the mortality resulting from low lethal temperatures was completed. For the higher critical temperatures, mortality developed more slowly. These experiments were summarized and published by Yuill (139).

> "When larvae are subjected to a temperature of 0°, within the upper critical range, - - the death rate increased rapidly up to two hours, and then continued to rise more gradually up to the seventh or eighth day.-- Prolonged exposure at 0° had a pronounced inhibitory effect upon the subsequent development of the survivors, for none of the larvae that were alive after an exposure of 6 days or more were able to reach the pupal stage when returned to developmental temperatures."

Figure 19 .-- Mortality of Dendroctonus brevicomis larvae under constant exposure to a temperature of 0° Fahr.

> "At -7½°F. practically all individuals were killed by exposures of 1 or 2 hours.
>
> "In general then, it seems that for western pine beetle larvae the length of time they are subjected to lethal temperatures influences mortality only at points in the upper critical range; and at all other points the intensity of the cold, rather than the period of exposure, is the governing factor."

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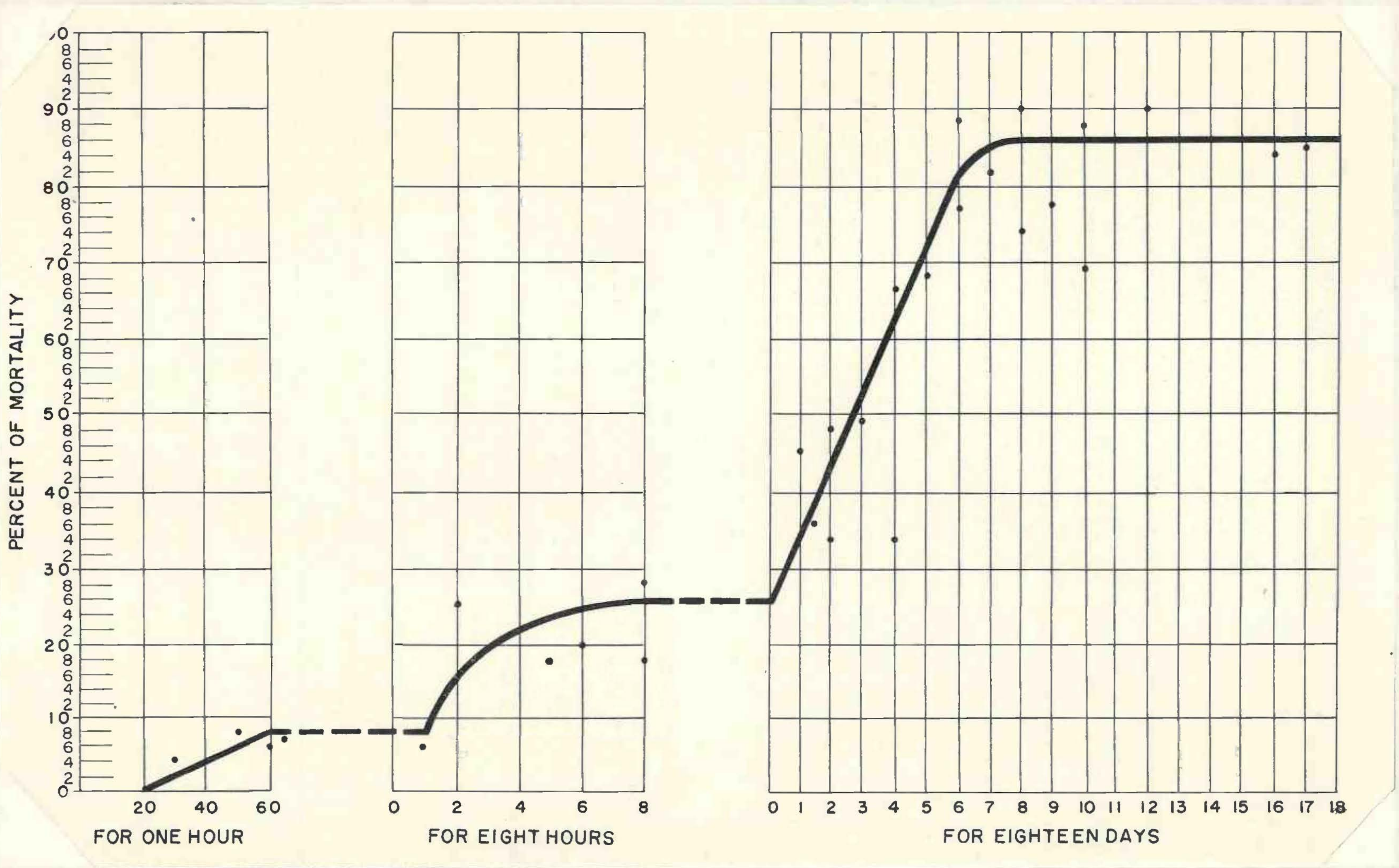

Figure 19.- Mortality of *Dendroctonus brevicomis* larvae under constant exposure to a temperature of 0° Fahr.

Critical low temperature for eggs, pupae, and adults.—Beal (U6) found that eggs did not incubate when kept at temperatures below 50°F. Miller (U194, ~~88~~) conducted laboratory experiments to determine the mortality of eggs in green phloem when exposed to steadily lowering temperatures. He found that high mortality occurs when eggs are exposed to temperatures below 0°F.; only 50 percent of the eggs incubated after short exposure to a temperature of -5°F.; and those exposed to -10°F. suffered a mortality of 90.7 percent. In general, eggs have been found to respond to the same developmental temperatures as the larvae, and are killed by the same lethal temperatures.

Miller (U194, 88) first reported that "pupae are somewhat less resistant to cold than larvae, as mortality was practically complete at -5°F." Later, however, Miller and Struble (U196) ran carefully checked parallel tests of larvae and pupae under identical conditions of exposure and found no difference in cold resistance between these two stages. "The range of critical temperatures and the ultimate killing points are essentially the same."

Miller and Struble (U196) checked the critical range for adults by testing 754 mature adults and found that mortality first appears at 14° and is complete at 10°F. Difficulties of determining whether adults shocked by cold were still alive were described.

> "The actual mortality was very difficult to determine, many of the beetles exposed to temperatures at 12 and 14° being moribund for long peridds and showing barely perceptible movement (of legs and antennae). However, the recovery of the beetles from exposure to 15°F. was quite definite as all became active in one-half hour when returned to warm temperatures. Also complete mortality at 10° was quite positive. Adults suddenly exposed to this temperature died with wings spread as though they had tried to fly before becoming thoroughly chilled."

Studies of field conditions which modify the effects of critical low temperatures.--

Relation of air and bark temperatures.-- Very early in the low temperature studies, attention was given to the differences between minimum air temperatures and the corresponding temperatures reached in the bark of standing infested trees. The insulating effect of the bark was considered to be an important factor in protecting the larval broods when lethal temperatures were reached in the surrounding air.

The first comparisons of air and infested bark temperatures were made by J.C. Evenden and H.J. Rust near Coeur d'Alene, Idaho, in December, 1926. During periods of sub-zero weather, mercury bulb thermometers were imbedded in the bark on both the north and south sides of infested trees and their readings compared with those of thermometers suspended in the air immediately adjacent to the bark thermometers. These tests were reported upon by Rust (U242). It was found that when air temperatures reached a minimum of -6° F. the bark temperatures were about 10 to 12° warmer; and when air temperatures began to rise from this point, the bark warmed more slowly and for a short time was even colder than the air.

The next comparisons of air and bark temperatures during sub-zero cold periods were made by Beal (3, Ull) in February 1933. Using bulb thermometers and the same technique as Rust, he obtained a series of readings from six infested trees on the Ochoco National Forest. With a minimum air temperature of -26°F., minimum bark temperatures varied from 0 to -17°. This variation in bark temperatures was largely attributed to differences in bark thickness. In thick-barked trees, the spread between bark and air temperatures was much greater than in thin-barked trees. In bark one-half inch in thickness, the minimum temperature reached was 8° higher than the air temperature; but in bark from 1 and 5/8 to 2 inches in thickness, the bark was from 26 to 29° warmer. Beal also found that the lag of bark temperatures behind changing air temperatures increased with bark thickness. In bark one-half inch thick, the temperature lagged one hour behind rising or falling air temperatures; but in bark two inches thick, the lag was two hours. In summarizing Beal stated: "The spread between air and bark temperatures is governed chiefly by bark thickness and the rate of temperature change. The lag in reaction of bark to air changes depends principally upon bark thickness."

In 1935 Salman initiated a study of comparative bark and air temperatures at Hackamore, California, using specially designed Foxboro anti-ambi compensated thermographs which gave a continuous record of bark temperatures. The bulbs were installed in the bark at a height of ten feet from the ground; a Friez hygrothermograph recorded air temperatures at a nearby point. Three bark temperature records and one air temperature record were maintained through three consecutive winters; in addition, minimum bark temperature records were obtained from seven infested trees within the same local area.

Figure 20.--Recording thermometer and emergence cages on ponderosa pine infested with western pine beetle to determine effect of temperature on emergence.

The data obtained in the Hackamore study were subjected to statistical analysis in a report by Salman and McLees (U274). They found that:

> "1. A close association exists between minimum air temperatures and minimum bark temperatures." [A correlation coefficient of 0.953 was found.]
>
> "2. Minimum bark temperatures may be estimated from minimum air temperatures (at least through the range of temperatures included in these tests, which ranged from + 61° F. to -30° F.) with an accuracy equal to a standard error of estimate of ± 4.70° F.

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Figure 20 .-- Recording thermometer and emergence cages on ponderosa pine infested with western pine beetle to determine effect of temperature on emergence.

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> "3. By elimination of one or more of the chief factors that contribute to the error of estimate, it is possible to reduce the standard error by from 0.6 to 2.9° F. Of these factors, daily temperature trends, variations in the conditions surrounding and inherent in individual trees, and the amount of daily temperature range appear to be the most important. Each of the last two factors contribute approximately one fourth of the standard error of estimate.
>
> "4. The relation of minimum air to minimum bark temperatures changes along the temperature scale." [At Hackamore, with minimum air temperature of 60° F., the bark was 11° F. warmer; at -30° F. the minimum bark temperature was 24° F. higher.]
>
> "5. The relation between air and bark temperatures is statistically very highly significant. A similar clear relation seems to exist between mortality and bark temperature or the temperature of exposure."

Tests of brood mortality at given temperatures of exposure showed a standard error of estimate of ± 4.87° F. or a range of about 9 percent. So it was stated by Salman and McLees that "It is not established ..... that brood mortality can be estimated from air temperature records without considerable error. Such estimates will be of most value when temperatures are low enough to produce considerable mortality and of least value when they produce but slight mortality."

Relation of bark thickness to brood mortality.— In many of the field studies of brood mortalities that have been made following cold weather, the actual temperatures reached in the bark were unknown; but a great deal of work has been done to determine the relation of mortality alone to bark thickness. In appraising the effects of the low temperatures of December 1932 on the Modoc National Forest, Salman (U253) analyzed 115 bark samples containing 6,543 dead and living larvae and found a fairly consistent relation between bark thickness and brood mortality; in bark thickness of one-inch or less, the mortality averaged 99.5 percent; while in bark thickness of 2 to 2¼ inches, the mortality averaged 39.4 percent, with most of the intermediate thicknesses falling into line with this trend.

Keen and Beal (U144) went into the bark thickness factor quite thoroughly in studying the effects of the 1932-33 sub-zero temperatures in Oregon. They examined 1,200 bark samples containing 147,619 living and dead larvae and found bark thickness to be the most important factor modifying the effects of air temperatures upon the broods. Mortality varied inversely with bark thickness; that is, for the same temperatures within the critical range, the thicker the bark the lower the mortality. The texture of the bark, whether hard and flinty or soft and spongy, also appeared to be important, a much higher survival being found in the latter. But on the whole, the actual importance of bark thickness is not as great as might be expected, since Keen and Beal found that in eastern Oregon practically 95 percent of all infested pine bark is from 5/8 to 1½ inches in thickness and the occasional extremes below and above this range can have only small effect in modifying the overall average mortality. But it is of extreme significance in survival of species.

In his report upon the effects of the 1932-33 freeze in northern California, Furniss (U63) stated:

> "It has been observed in trees with very thick bark, often deeply ridged, that the brood tends to become localized in the vicinity of the crevices, thus tending to lessen the effective protective layer. Thus it is conceivable that a tree of uniform thickness might protect the brood to a greater extent than a tree with deeply ridged bark but of much greater average thickness."

Furniss (U66) studied the effect of a low temperature of -27°F., which occurred in eastern Oregon in November 1935, upon brood mortality and the insulating effect of bark. He found that in general brood mortality varies inversely with the amount of insulation offered by bark except that brood with only ¼ inch bark insulation suffered less than those with ½ inch insulation. He found that brood mortality bears a direct relationship to the position of brood with reference to the inner bark surface - the nearer the inner bark surface, the greater the mortality. He states that approximately 90 percent of the overwintering third and fourth instar larvae occur within ¼ inch of the inner bark surface.

Keen and Furniss (75) took into account the depth of larval broods in the bark and determined the average thickness of bark covering the various brood stages. From weighted averages, they determined that "in central Oregon 95 percent of the overwintering broods are protected by one inch or less of bark." In summarizing all of the mortality studies of preceding years, these authors concluded:

> "In general, mortality from freezing varies inversely with the thickness of the bark in which the brood occurs —. The same relationship is evident when the amount of absolute insulation is considered, although the correlation is not good for insulation of less than 1 inch."

But it was also found that a higher mortality occurred among larvae living in or near the phloem area than in the outer bark, regardless of the fact that the larvae in the phloem were protected by a greater bark thickness. This was attributed to the high moisture content of the phloem which has been shown to affect the cold resistance of broods unfavorably; and also the fact that the small larvae in the phloem region do not develop the same degree of cold hardiness as mature larvae.

Duration of cold periods.— As in the laboratory experiments, the time factor was found to be highly important in the field in modifying the effects of critical low temperatures. The longer sub-zero temperatures prevail, the more nearly do the bark temperatures and the body temperatures of the larvae tend to come into equilibrium with that of the surrounding air. Keen and Furniss (75) summarized this point thus: "The data, although not conclusive, indicate that given the same minimum temperature the prolonged cold was most effective, the unseasonable cold less effective and the brief cold least effective in reducing western pine beetle populations."

Moisture conditions in the bark.— Miller (88,U194) found that larval broods in saturated bark succumb to temperatures some 10° higher than broods in normal dry bark. That excess moisture may reduce the degree of cold hardiness seems reasonable in view of the theory that the insect must regulate the amount of free water in its body tissues and reduce water content of the cells in order to avoid freezing. As suggested by Keen and Furniss (75) this factor over-balances that of bark insulation and explains the high mortality of young larval broods in the phloem area. On the Ochoco-McKay Creek control project in central Oregon during the winter of 1932-33, it was the dry partially abandoned trees in which broods survived the cold to the best advantage. According to Keen (U147):

> "The heaviest loss from winter killing occurred in the broods of small larvae in the inner, moist bark of green trees. Thus small larvae in the moist inner bark, close to the wood and supposedly protected by a thicker layer of bark were killed more readily than full grown larvae in the outer, dry bark, with apparently much less bark protection."

Height on the tree.— During periods of cold weather with quiet air and temperature inversion it has been found that it is colder near the ground than higher in the trees. In a study of temperature differentials throughout a forest drainage, Keen (U153) found that "the tendency was for the temperature to rise as one progressed up the tree. There was a significant difference between the 10 foot level and the higher levels, but no significant difference between the 40 and 70 foot levels. These higher levels tended to be from 0.5 to 0.7° F. warmer than the 10 foot level."

During freezes caused by cold air masses accompanied by high winds, temperature inversion does not occur. In such cases, Keen and Furniss (75) found that "winter killing at the base of trees averages 19.7 percent less than the general average for the entire tree; above the base the mortality rate is uniform for bark of the same thickness."

This might be due to warmer temperatures near the ground, or possibly to the character of bark, since bark of the same thickness was compared.

North and south exposures on trees.— In the temperature differential study, Keen (U153) found no difference in temperature between the north and south sides of trees during two periods of extremely low temperature, when the air was still.

However, Keen and Furniss (75) found a significant difference in brood mortality, following freezes with strong wind movement, between the north and south sides of the same tree.

> "Brood mortality is consistently greater on the north than on the south side of infested trees following periods of cold weather. This is well illustrated by a statistical analysis of 145 tree samples in the winter of 1932-33 ---, mortality on the north side was found to be 30 percent greater than on the south side."
>
> "Minimum temperatures reach about the same level on both sides, but on bright days temperatures do not rise as rapidly or as much on the north as on the south side; therefore the duration of cold is much longer on the north. The second consideration is that because of generally colder conditions on the north side, the brood does not develop as rapidly, over-wintering larvae are smaller, and in addition the bark is tighter and more moist."

Beal (U11) found that during bright days of sub-zero weather the sun, both directly and by snow surface reflection, warmed up the bark on the south side as much as 16° above that of the air temperature.

Tightness and texture of bark.— The only observation on this point has been made by Keen and Furniss (75,U66). "Brood in trees with tight bark is less resistant to freezing than brood in trees with loose bark." This is probably due to a correlation between tight bark, its moisture content, and younger age of brood. Bark texture was considered to be unimportant.

Topography, elevation, and wind movements.— The distribution of minimum temperatures within a general watershed of 138 square miles on the Ochoco National Forest, Oregon, was studied by Keen (U153) to determine whether the Weather Bureau records usually made available at towns and population centers can be used as a reliable index to bark beetle mortality in nearby forested areas during periods of extremely low winter temperatures.

The two cold periods studied occurred during November 1936 and January 1937. On November 2, 1936 the temperature dropped to 5.0°F and on January 8, 1937 to -27°F. at Ochoco Ranger Station. A preliminary examination (U44) showed 46 percent of the large western pine beetle larvae were killed. The low temperatures occurred during clear, still nights with little or no wind movement. This brought about typical temperature inversion with the coldest layers of air settling in the valleys and warmer air moving to the higher levels. This was in direct contrast to the prior cold period of December 1932, when a cold air mass moved in, "a strong wind blew more or less constantly, resulting in a thorough agitation of the air, so that similar temperatures prevailed over wide areas."

With these conditions of temperature inversion, it was found that temperatures increased from low to higher elevations. "Valleys were consistently colder than slopes or ridges, but the differences between south slopes and north slopes were so slight that they could hardly be considered significant. Ridges tended to be colder than slopes. It was warmer high on the tree's bole than near the ground, but no difference was found according to side of tree." The total spread in temperature between all of the 144 thermometers used in the experiment was 19°F. in the November cold spell and 22°F. in the January cold period. The maximum difference between any one reading and the base weather station (within the area) was 13°F, while the greatest average difference of any one elevational ? zone and the base weather station was 10.8°F. On the average, the forested area was found to be about 5°F. warmer than the valley where the base weather station was located, but only 1.7°F. to 2.5°F. warmer than the nearest standard weather station located in a town some 27 miles distant.

It was pointed out that the base station located in a valley was a poor indicator of the variable temperatures which may occur within a neighboring area, and the beetle mortalities which may occur in different local spots, especially in cases where the border line of lethal temperatures was concerned.

In summarizing this study, Keen stated that:

> "This low temperature experiment showed that during cold spells without wind movement there may be wide temperature differences throughout a drainage area of 138 square miles, sufficient to cause considerable variation in bark beetle mortality within the area, but that for the forest area as a whole the average temperature may be reasonably close to that shown by nearby standard weather stations. If the average low temperature differential between a given forest area and its nearest standard weather station is determined, then it should be possible to estimate the general bark beetle mortality on the area following a cold period with a reasonable degree of accuracy."

The general effect of low winter temperatures on bark beetle populations.-- In spite of all the modifying factors of brood condition, bark thickness, moisture, exposure, length and duration of cold spells, the overall effect of low winter temperatures in killing western pine beetles can be estimated within reasonable degrees of accuracy. From a large number of examples of minimum air temperatures and the corresponding brood mortality found during three periods of cold weather in eastern Oregon; i.e. a period of prolonged cold in December 1932, a short period of intense cold in February 1933, and a period of unseasonable cold in November 1935, Keen and Furniss (75) showed that a fairly close relationship existed between the minimum air temperatures reached and the percent of brood mortality which occurred as a result. The relationship of air temperature to brood mortality which may be expected is shown in Figure 21 . It is evident from this graph that within rather broad limits the amount of brood mortality can be determined approximately if the minimum temperature reached during any given cold period is known. This chart should be helpful in estimating the probable effect on western pine beetle populations of any low winter temperatures reported by the Weather Bureau from ponderosa pine forest areas.

Figure 21 .—Relation of air temperature to western pine beetle mortality.

Regardless of the very high mortality that has been recorded following some of the more severe cold spells in the pine type, western pine beetle populations were not eliminated, and although greatly reduced at first have shown an amazing capacity to recover their numbers within a year or two.

In appraising the effects of the 1932-33 winter kill in both Oregon and California, Keen and Furniss (75) stated: "For the entire area affected, the 1933 infestation was lower than in 1932 and considerably lower than it would otherwise have been as indicated by the general infestation trend." And in summarizing the results of a series of studies, these authors also stated:

> "In general, the effects of low temperatures are not so evident in the infestation trend except in extreme instances, about once in 10 years, when the course of the infestation may be altered for about 1 year. Anything less than 50 percent reduction has little or no effect upon the annual infestation; therefore, this amount of kill, or more, is necessary to cause alteration of artificial control work."

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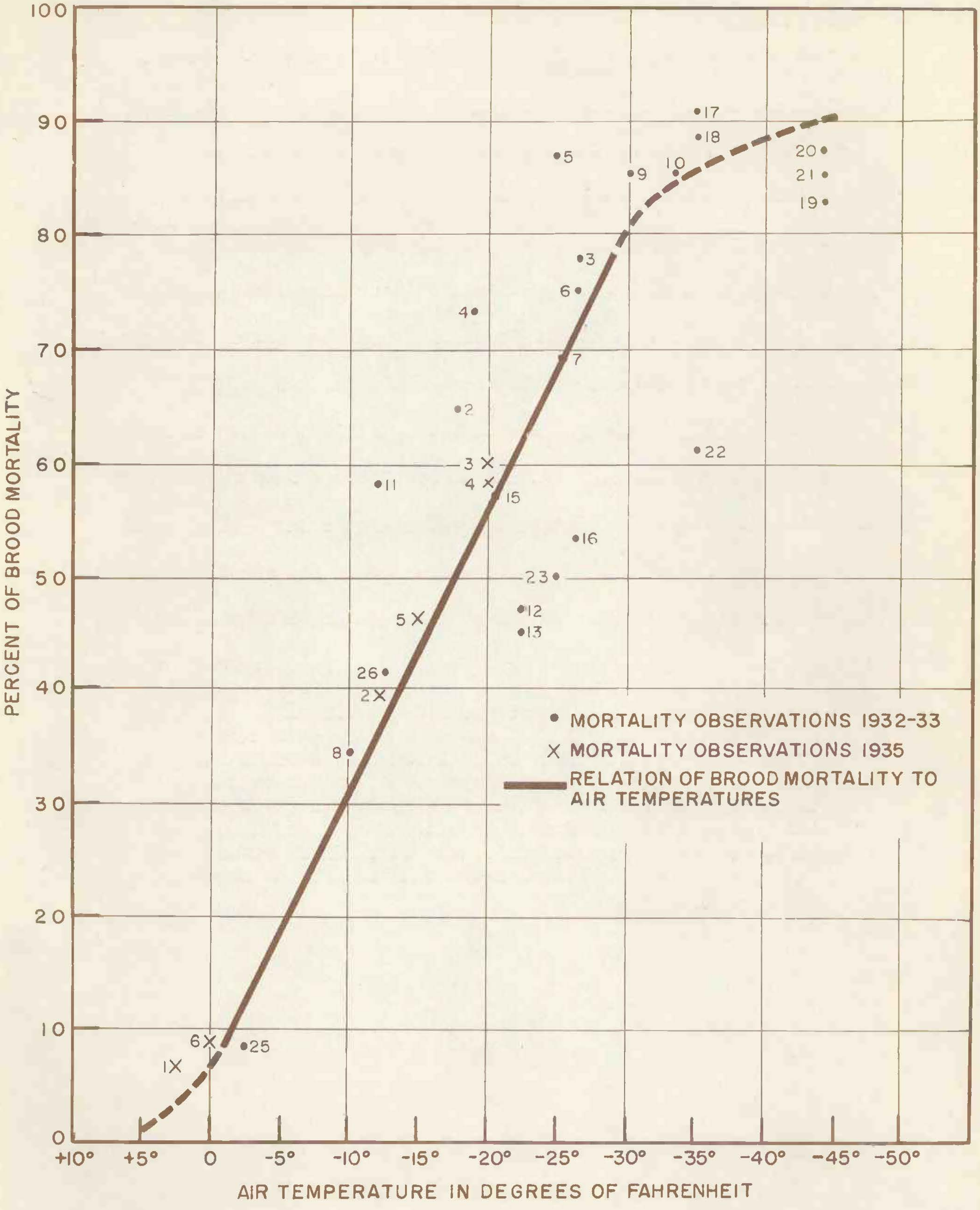

Figure 21 .-- Relation of air temperature to western pine beetle mortality.

Lethal High Temperatures

Scope of investigative work.-- In 1915 Keen (U126) noted that in an infested log which was lying in a position exposed to the sun, no emergence occurred ~~in~~ from the bark on top of the log, but there was a fair number of exit holes on the underside. He, therefore, concluded that "the bark becomes so heated in the summer sun that the beetles either fail to develop or are killed." He also tested the effects of solar heat upon the adults: "One hundred fifty D. brevicomis were placed on a pine board in the sun. All died within about 20 seconds. The temperature (air) was about 95°, but the board was considerably hotter."

Following these first observations, the possibility that solar heat could be used in the control of the western pine beetle was apparently overlooked until 1919. During the late spring of that year the exposure of infested bark to the sun was incidentally used by Albert Wagner to destroy broods on a control project on the Sequoia National Park. As the hazards of burning infested bark increased in late April and May, a number of infested trees which had been felled and peeled were held awaiting more favorable weather for burning. Wagner noted that the broods in pieces of bark which lay exposed to the sun died within a few days. He then spread all of the infested bark to the sun with the result that practically all of the broods were killed without burning.

The prospect that solar heat could be used in lieu of burning stimulated a series of experiments that were carried on near Ashland, Oregon, by Miller (U179) and Patterson (U206).

In 1920 and 1921 further experiments with high temperatures were carried out near North Fork, California; the results of which were later included in a summarization of the work on high and low lethal temperatures and published by Miller (88).

The critical high temperatures.-- In summarizing these studies it was shown that in the laboratory exposed larvae first begin to show the effects of heat at temperatures of 95 to 100°F. when sluggishness and decreasing activity set in; above 100° F. activity ceased altogether. When larvae were exposed to currents of warm air, which produced low humidity and rapid evaporation, they became paralyzed and did not recover after 30 minutes' exposure to temperatures of 100 to 105°F.

When normal humidity was maintained in sealed containers, simulating conditions in the larval and pupal cavities in the inner bark, high temperatures took effect more slowly; slight activity continued up to 105°. Heat paralysis set in after several hours' exposure at 108 to 110°F. from which the larvae were able to recover when brought back to normal temperatures. Above 110°, the temperatures were usually fatal. Heat paralysis set in after 20 minutes' exposure at temperatures between 110 and 115°, from which there was no recovery when returned to normal temperatures. No larvae survived even brief exposures at 118°F.

Field tests were run in which infested bark sections were exposed to the sun and the bark temperatures recorded by means of mercurial bulb thermometers imbedded in the bark. It was found that noticeable mortality first appeared when the bark temperatures reached 100°F., and that all larvae were killed when the temperature reached 120°, thus indicating a fairly wide range of [high-]critical high temperatures. The following records from a typical test run between the hours of 9:30 A.M. and 11:30 A.M. on June 23, 1920, illustrate the mortality that was found as the bark reached certain temperature points within the critical range.

Time	Temperature recorded in bark	Mortality of larvae
9:30 A.M.	76° F.	1.3%
10:00 A.M.	100° F.	34.2%
10:30 A.M.	109° F.	78.0%
11:00 A.M.	118° F.	94.0%
11:30 A.M.	120° F.	100.0%

During the period of this test, air temperatures ranged from 78 to 80°. Because of variations of bark thickness and moisture, the actual temperatures throughout the bark may have differed from those recorded by the bulb thermometer; this accounts for the differences between mortalities found in the bark and those found at similar temperatures with larvae exposed to air temperatures in the laboratory. It is fairly well established, however, that the critical high temperatures for larvae range from 100 to 115° F.

Beal (U6) found that at sustained high temperatures between 102° and 106° F., all eggs were killed.

Effect of solar heat on broods in infested trees.— Little evidence has been presented to show that any appreciable mortality occurs in beetle populations in their natural environment in the field as a result of hot weather. This can be readily understood if we consider that the beetles for most of their existence in all stages are found in standing infested trees. The bark surface of these trees is in a vertical position so that through the hottest part of the day there is a high angle of incidence to rays of the sun. It was shown by experiments that in order for the bark to absorb a great amount of solar heat, it must be exposed with its surface approaching a right angle to the rays of the sun. Added to this factor is the fact that infested bark in standing trees is usually shaded through part of the day by limbs and foliage; and during periods when it is exposed to the sun, the insulating thickness of the bark protects the brood long enough to prevent fatal temperatures. In standing infested trees, we find that records are altogether lacking of brood mortality which can be attributed to the effects of solar heat.

Some mortality may occur, however, when infested trees fall so that the prostrate trunk is exposed to the mid-day sun. This happens but rarely in nature. In the case of green trap logs which are attacked after they fall, it has been found that the beetles attack only on the underside of the log or shaded bark areas, and no brood develops in that part of the log exposed directly to the sun.

Nutritional Deficiencies

Only a preliminary start has been made upon the actual nutritional requirements of the larvae and these have been covered in the discussion of food habits of the larvae on page 60 . Jeffrey (U103) found that after the larvae feed for a time in the inner bark there is a marked reduction in sugar concentrations which apparently explains why the larvae migrate to the outer bark. However, the part that unsatisfactory food conditions may play in bringing about mortality of the broods has not been investigated and little can be stated in regard to this factor. It has frequently been observed that certain trees produce bigger and better beetles in greater numbers than others and it can be superficially assumed that this is due to varying nutritional conditions. But on the basis of the very limited information on nutritional requirements of the western pine beetle, this assumption can be nothing more than conjecture.

Competition for Food Supply

The most important feeding period for insects comes during the larval period; and when there are more insects than available food to carry them all through to the final stages of larval development, some must inevitably die of starvation. This is especially true of the western pine beetle where the larval existence is definitely circumscribed within a very small area. The female largely determines this area when she deposits the eggs, and the larva must find its entire food supply within an inch or two of the egg niche where it begins its existence. It has no choice of shifting to a new location if the food supply in the inner bark begins to run low.

Competition between individuals of the same broods.— As has already been mentioned under "Density of attack," the adults normally space their attacks over the bark surface so that there will be sufficient food to carry the broods through complete development. At times, however, what appeared to be overcrowding of the attacks has been noted. This has occurred when there was a high concentration of adults in local areas. Under these conditions, attacks and egg galleries were very closely spaced with the result that there was a high larval mortality. One such case in the California windfall area in 1921 was reported by Miller (86) where the attack was estimated to be about twice as heavy as normal and the emergence of new adults about half of normal. It was inferred that the broods were reduced as a result of starvation.

However, the actual effect of over-crowding of attacks upon brood mortality has not been subjected to critical study and there is little evidence to support the theory that competition is of any importance as a natural factor of control. In his analysis of brood statistics, Keen (U138) plotted the number of beetles attacking and emerging on the Jenny Creek unit from 1917 to 1926 and concluded: "This graph indicates that, to some extent at least, the emergence is influenced by the number of beetles attacking --- a low attack producing a low emergence and vice versa. These records do not indicate that overcrowding of attacks, such as occurred in 1925, is detrimental to good brood development."

The great variation that has been found in the number of beetles emerging from a square foot of bark, regardless of the number that attack, leaves some doubt as to what constitutes normal stocking. We do not know the actual number of larvae per square foot which can be adequately nourished in that much bark surface. On the whole, we can assume that over-population occurs rarely since the parent beetles usually have ample opportunity to disperse their attacks, both in the trees and over the forest, so that their progeny are assured of ample food supply.

Competition with other cambium feeding insects.— The larvae of large beetles which attack recently infested trees and feed in the phloem area become a competing factor when these insects consume the food supply of the inner bark before it can be utilized by bark beetle broods. Most of the competition from this source has been attributed to the cerambycids. Hopkins (42) first recognized the importance of these beetles. "The so-called *robbers* consist of large bark-boring grubs or larvae of long-horned beetles (Cerambycids) which sometimes rob the bark beetle larvae of their food supply or kill them outright by destroying the inner bark before the broods of bark beetles have completed their development." Blackman (5) found *Acanthocinus spectabilis* Lec. especially effective as a robber of the Black Hills beetle. He also listed *Monochamus maculosus* Hald., *Asemum atrum* Esch., and *Tetropium velutinum* Lec.; but considered the latter two species of lesser importance since "they are considerably smaller, do not occur in so many trees, and are found principally in the lower trunk."

In referring to *Acanthocinus spectabilis*, Keen (61) stated that the "larvae feed in the inner layers of bark, often consuming so much of it as to starve out the bark beetle broods."

Person (U232) compared the western pine beetle emergence from bark that had been heavily mined by cerambycids with emergence from bark in which there was little or no cerambycid work. From a series of four trees on the Cascadel area, he selected 34 square feet of bark and analyzed the attack and emergence of the western pine beetle.

No. sq. ft. of bark	% of inner bark mimed by borers	*D.b.* attacks per sq. ft.	*D.b.* emergence per sq. ft.
17	8	14	60
17	56	12	37

Person's conclusions were that "the averages for the 4 trees show that the emergence from sections with little or no cerambycid work was almost twice as high as from sections on which the cerambycids had destroyed on the average about 56 percent of the inner bark." Person attributed all of the borer work to *Acanthocinus spectabilis*.

> "As these larvae were a number of times larger than *D.b.* larvae, they would naturally destroy large quantities of their food and would probably kill many of the *D.b.* outright when they happened to get in the way of their (the cerambycids') large mandibles.---
> To be of importance they must begin work in the phloem while the *D.b.* brood is still small and before it has worked out into the outer bark where it is safe from the cerambycids."

In 1933 Furniss (U64), working with J.W. Bongberg, made a preliminary study of the life history of *Acanthocinus spectabilis*. He found that *A. spectabilis* and *A. obliquus* both infest approximately the same bark area that is attacked by the western pine beetle. "*A. spectabilis* characteristically infests the lower bole where the bark is thick while *A. obliquus* is commonly found in the upper portions of the stem where the bark is thin." Available data in one case indicated that *A. spectabilis* had developed and emerged in four months. However most of the brood apparently requires one year to complete the life cycle. Furniss concluded that:

> "The effectiveness of *Acanthocinus* as a control factor of the pine beetle is bound up directly with its ability or inability to follow *Dendroctonus brevicomis* into the trees almost at once and to develop rapidly. The fact that the pine beetle larvae mine into the outer bark upon hatching makes the Cerambycid work much less a natural reduction factor than when in association with a species such as the Black Hills beetle, the broods of which confine their activities to the phloem region almost entirely."

Parasites

The records accumulated over a period of some 30 years fail to indicate that parasitism plays any important part in the natural control of the western pine beetle. In fact any records of specific parasitism are rare, although investigators have maintained considerable persistence in the search for evidence of effective parasitism in working over the vast amount of brood material that has been analyzed in connection with various mortality studies.

Webb (133) does not mention parasites but does refer to the work of the clerid predator. Hopkins (42) mentions parasites only in a very general way in discussing the natural control of *Dendroctonus* beetles. The first records of what were thought to be specific parasites were made by Keen (U126) when, in connection with life history studies, he found the adults of three species of chalcids. Keen suspected that these were parasites of the beetle because they belong to a group of insects which are mainly parasitic and because they were found either ovipositing in, or were reared from, bark infested by *D. brevicomis*.

Later collections and rearings of these same species by other investigators confirmed the fact that they are to be found occasionally in connection with *D. brevicomis* broods; and that they are probably true parasites. Person (U231) made a summary of available notes up to 1928 on parasites of *D.b.* and concluded that "a few parasitic species are almost always found with *D. brevicomis* but not in sufficient numbers to be of much importance." Miller (U198) summarized the Hopkins notes on probable parasites and obtained the following information:

> "1. *Cecidostiba burkei* Cwfd. has been found ovipositing through bark infested by *D. brevicomis* broods and has been found in cages containing infested bark in rearing. One case is recorded of the adults being taken from pupal cells of *D. monticolae* in lodgepole pine with remains of host. It has also emerged in cages containing sugar pine logs infested by *D. monticolae*.
>
> "2. *Cecidostiba dendroctoni* Ashm. has emerged in a cage containing bark infested by *D. brevicomis*; was also found on brood log of *Scolytus ventralis*.

> "3. Eurytoma sp. was found ovipositing in bark infested by D. brevicomis and was reared from bark infested by flatheads. It may or may not be parasitic as the species of this genus vary from parasitic to phytophagous.
>
> "4. Pachyceras eccoptogastri Ratz. The best case for parasitism has been established for this species. It has been found ovipositing in, and has also been reared from, bark infested by D. brevicomis. In two cases larvae and pupae were isolated from larval cells of D.b. and reared through to adults. One record indicates that it is also parasitic on Ips oregoni."

Altogether the total number of Hopkins notes collected since 1915, representing intensive work by a number of investigators, records only 19 cases of suspected parasitism. This scarcity of records over a long period of years can be interpreted as evidence that parasites are a negligible factor in the biological control of the western pine beetle.

Predators

In contrast to the scarcity of parasites, predators of the western pine beetle are common. Predators, including birds and a long list of predatory insects, are undoubtedly an important factor of natural control.

Birds.— The work of woodpeckers on advanced larvae and pupae in the outer bark of infested trees attracted the attention of the first investigators. In Idaho, Webb (133) observed that "the work of woodpeckers was found upon most of the trees that had been killed by D. brevicomis and these birds had evidently destroyed a large percentage of the insects in some of the trees." Hopkins (42) discussed the importance of bird predators, but concluded that "birds evidently render the greatest service when but few trees are being killed - - where many hundreds of thousands of trees are being killed, the limited number of birds can have little or no effect."

In the first western pine beetle control project on the Klamath National Forest, 1911-12, records were kept on the abundance of woodpecker work in all treated trees. Burke (U43) summarized the records from 679 trees and found that the amount of woodpecker work had been recorded as light on 13 percent, medium on 39 percent, heavy on 1 percent, and none on 47 percent of the trees.

Keen (U126) undertook to determine the actual percentage of brood destroyed by woodpeckers. By comparing the emergence from bark samples that had been heavily worked by woodpeckers with the emergence from undisturbed bark, he found an emergence of 20.2 beetles per square foot from the former as against 75.2 beetles from the unworked bark, indicating that the woodpeckers had reduced the brood by about 73 percent.

Buckhorn (U39) investigated the effectiveness of woodpeckers on the Ochoco National Forest in 1934 by placing a two-foot tree trunk cage over bark which had been 70 to 85 percent stripped, thus reducing it from 1¼ to ¼ inch or less in thickness. Next to this was a similar cage covering undisturbed bark. From the undisturbed bark, 370 beetles per square foot emerged, while on the area worked by the woodpeckers 103.5 beetles per square foot emerged - a reduction of 72.1 percent. (Figure 22)

Patterson (U211) pointed out that the woodpeckers are known to feed not only on various species of bark beetle broods in the bark, but also on Cerambycids and Buprestids. Woodpeckers accomplish the greatest good during the winter months when they feed upon the dormant bark beetle broods; also they feed on beneficial insects as well as the destructive ones.

Figure 22.-- Patches of outer bark stripped by woodpeckers is characteristic of western pine beetle infested ponderosa pines.

Page 207a follows.

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Figure 22.--Patches of outer bark stripped by woodpeckers is characteristic of western pine beetle infested ponderosa pines.

Patterson was of the opinion that the most important woodpecker predators of the western pine beetle were the following (in the order named):

1. White-headed, Dendrocopos albolarvatus
2. Modoc, Dendrocopos villosus orius
3. Gairdner's, Dendrocopos pubescens gairdnerii
4. Arctic three-toed, Picoides arcticus
5. Williamson's sapsucker, Sphyrapicus thyroideus
6. Western pileated Dryocopos pileatus picinus

All of these species are more or less common in the transition zone of Oregon and California.

Person (U229) made a study of woodpecker activities on the Cascadel unit of the Sierra National Forest, California, in 1926, giving special attention to the extent to which these birds feed upon the beneficial clerid and ostomid insects found with D. brevicomis broods. Person determined the species of woodpeckers feeding on infested trees in this area during the spring, summer, and fall period; these were the western pileated(Dryocopos pileatus picinus), the white-headed woodpecker (Dendrocopos albolarvatus),and the Hairy woodpecker (Dendrocopos villosus).

Person recognized the western pileated woodpecker as the most beneficial bird predator when abundant enough to be a factor, because it thoroughly chisels off the outer half to three-quarters of the bark over large bark areas. He compared brood counts from bark sections that had been worked by this woodpecker with unworked sections and found that in the former the surviving brood was only 16 percent of normal. He also found that the bird had reduced the clerid predator population until it was 30 percent of normal.

The hairy and white-headed woodpeckers were found to be less thorough in working over the bark and were inclined to take only those insects nearest to the bark surface. A stomach examination of each species showed that they feed upon D. brevicomis, clerids, cerambycids, and other associated injurious and beneficial insects quite indiscriminately.

In a series of three trees that were analyzed, Person found that the hairy and white-headed woodpeckers selected the clerid Enoclerus lecontei Wolc., which pupates near the bark surface while much of the D.b. brood deeper in the bark had not been disturbed. In brood counts from 136.5 square feet of bark samples from these three trees, it was found that the woodpeckers destroyed nearly 10 percent of the beneficial clerids and only a negligible number of D. brevicomis.

Mammals.-- Rust (U244) found that when broods of the mountain pine beetle were exposed by the peeling method of control, the broods were usually carried off by ants and centipedes and were eaten by small mammals, such as chipmunks and mice. There is little possibility of rodents doing anything like this with the western pine beetle because the broods are effectively protected by the outer bark. Rodents may capture a few adults of the western pine beetle while they are crawling around in the duff during the attack period, but any evidence of this habit is yet to be obtained.

Insect Predators.--

Review of investigations of predacious insects.-- Insects that prey upon the western pine beetle have been the subject of much detailed investigation. Clerid beetles especially aroused the interest of the early investigators, probably because of the conspicuous habits of the adults in concentrating on trees that are being attacked by bark beetles, where they run actively over the bark surface, and capture Dendroctonus adults before they can burrow into the safety of the inner bark. In 1892-93, Hopkins (40) was so impressed with the European bark beetle destroyer, Clerus formicarius, that he introduced it into West Virginia to work on the southern pine beetle. The imported predator, however, apparently did not thrive in its new environment.

In the first studies in Idaho, Webb (133) reported that "larvae of predacious beetles of the genus Clerus (Enoclerus), which are known to prey upon Dendroctonus larvae, were quite common in and under the bark of infested trees and they doubtless help to some extent in keeping down the numbers of beetles." Detailed studies of the predacious insect enemies of the western pine beetle were begun in 1922 in connection with the Southern Oregon-Northern California Pine Beetle Control Project at Klamath Falls, Oregon.

In a preliminary report, Person (U224) listed some 10 species of beetles and one Rhaphidid which observations indicated to be predacious on Dendroctonus. This report included life history notes and the results of feeding experiments with the more important predators. Person pointed out that under the methods of peeling and burning all of the infested bark then used in direct control work, beneficial insects were being destroyed as well as the bark beetles. This discovery led to the practice in control operations of protecting from fire the bark and duff around the stump where the clerids concentrate to pupate.

In 1923 and 1924 (U227) Person's studies were continued at North Fork, California, where he carried on another series of experiments. A considerable amount of attention was given to feeding experiments to determine the capacity of the different species to consume adults and larvae of the bark beetle. Miller and Person (U184) found a positive correlation between the mortality of western pine beetle brood and the number of predators per square foot of bark at different heights on a tree.

Person (U231) summarized all of the work that had been done up to 1928 on parasites and predators of the western pine beetle. The report gave a complete account of the habits and seasonal history of *Enoclerus lecontei* based on five years of study, together with an account of experiments which were carried out to determine the actual effectiveness of this species as a predator.

In 1928, 1929, and 1930 the work was concentrated on *Enoclerus lecontei* and a series of experiments was conducted in biological control, which will be discussed under this species.

The blue-green trogositid, Temnochila virescens var. chlorida (*Mann.*).— This ostomid beetle is the most commonly observed predacious insect in or around trees infested by the western pine beetle and other bark beetles. The adult is from 10 mm. to 18 mm. in length and of an iridescent bluish-green color. These adults appear around infested trees soon after attack. They rest in bark crevices or crawl over the surface and actively prey upon any unwary bark beetles which may be loitering on the bark surface. *T. virescens* is by no means specific but will be found around trees infested by many species of bark beetles, cerambycids, buprestids, and other wood-boring and cambium-feeding insects. The larvae, which are also voracious general predacious feeders, are grayish-white at maturity and 25 to 30 mm. long. The head is black and flattened, the dorsal surface of the first three thoracic segments have black sclerotized plates, continuous on the first two segments and separated on the third. The dorsal portion of the last abdominal segment has a black hook-like process.

The habits and seasonal history have been quite thoroughly worked out by Person (U231) and Struble (119). *The eggs* are laid in groups of from 2 to 50, usually deep in bark crevices. According to Person (U231), who studied this species only in connection with the western pine beetle:

> "After hatching, the larvae work their way through to the inner bark, taking advantage of cracks between the bark scales and the entrance and ventilating holes of D. brevicomis. After reaching the inner bark, they begin to feed on the young D.b. larvae, following them as they work back into the middle of the bark. The larvae develop with the D.b. and feed upon the larvae, pupae, and new adults. They burrow their way through the bark at will, going from one D.b. to the next while feeding. They are cannibalistic in the larval stage. Only the larvae which hatch by July 1 complete their development during one season at Klamath Falls. The larval period varies from about 3 or 4 months for those that complete their development in one season to 10 or 11 months for those that overwinter as larvae.
>
> "The pupal stage is passed in an unlined cell in the middle of the outer bark at the place where the larvae finish feeding. The pupal stage of the individual lasts about 2 weeks (10 to 20 days).
>
> "The adults overwinter in the bark crevices of infested trees. The average adult life is about 4 months for those that do not overwinter, and about 10 to 12 for those that do."

In his studies of the biology of Temnochila virescens in association with the mountain pine beetle, Struble (119) found that the newly hatched larvae must feed within two weeks in order ✓ to stay alive, but once fed can live for 10 months or more without food. He divided the larvae into "short-term" and "long-term."

> "The short-term larvae comprising not over 5 percent of the total number studied, required from 10 to 12 weeks to reach maturity at 75°F. The long-term larvae required 30 weeks to reach maturity at 75° F., and 2 months under field conditions. The short-term larvae molted, consistently, five times during the course of their development. The long-term larvae were found to have an additional molt, with records of seven molts among some individuals. The cause of short-term development was not determined definitely, but studies indicated that it was not linked with the quantity of food eaten or with an hereditary strain."

Both Person and Struble found the adults to be voracious feeders. Struble found that in confinement they consumed from one to three mountain pine beetle adults per predator in a 24-hour period. Frequently as many as 15 adult bark beetles were killed, and many of these are eaten in a day by one large T.v. adult. Person found that in cages the average life of adults was over three months when fed on D.b. adults; the average number of beetles consumed over a long period was .935 daily. Person also observed that Temnochila adults feed on clerids and probably any other insect they can capture. Although T. virescens was at first thought to be the most effective predator of the western pine beetle, it was finally given up as a possibility for biological control because of its indiscriminate selection of hosts and its cannibalistic tendencies.

The black-bellied clerid, Enoclerus lecontei Wolc.— The black-bellied clerid has been found to be predacious on various species of Ips, Pityophthorus, and Dendroctonus; but in California, Oregon, and Washington it is found most abundantly with western pine beetle broods. Its biology and its effectiveness as a predator of the western pine beetle have been adequately covered in an article by Person (106).

The *adults* are very active and voracious and run rapidly over the bark surface during the period while trees are being attacked by *D. brevicomis*. Their movements somewhat resemble those of ants, although the clerids are more active. They grasp the pine beetle and suck the body juices, discarding the hard chitinized parts of the body. According to Person (*U231*), each clerid adult destroys at least 25 pine beetles during its active life of 6 to 8 weeks.

The *eggs* are laid on newly attacked trees in the tiny crevices between the bark scales. Usually from two to five eggs are laid in a single group, but as many as 10 have been found closely fitted together in a one-layered mass. Incubation requires from 10 to 14 days under average conditions of the active field season.

The larvae are pink in color, with characteristic anal hooks and scleritized parts dark brown. Upon hatching they enter the outer bark through a crevice or ventilation hole and are next found in the phloem or inner bark. Here they begin feeding on newly hatched D. brevicomis larvae, working their way through the bark from one larval mine to another, killing and consuming all of their victims with the exception of the strongly scleritized body parts. As the D. brevicomis broods develop and enter the outer bark, the clerid larvae follow them, and by the time the host larvae are mature, the clerid larvae have completed their feeding. At this point from 40 to 90 percent of the clerid larvae bore out through the bark and crawl to the base of the tree where they pupate in the outer bark scales near the surface of the ground or in the duff surrounding the stump. The remaining 10 to 40 percent remain where they completed their feeding, and pupate in the outer bark of the main trunk.

The pupae are formed in flattened oval cells hollowed out by the prepupal larva. These cells are lined with a white silvery substance which distinguishes them from the bare unlined cells made by Temnochila. The pupal period lasts from 6 to 14 days under active temperatures.

The seasonal history as worked out by Person (U231) is rather complicated and is only partially synchronized with that of the western pine beetle. In central California there are about two generations, but a certain percentage of the broods is retarded in development, and only one generations results. Their overwintering habits are such that there is a heavy concentration of clerids on the first seasonal generation trees of the western pine beetle. Person reports that the average number of clerid larvae per square foot of infested bark on first generation trees is nearly double the number found in trees of the second generation, and more than three times the number on trees of the third generation.

Person obtained some data on the effectiveness of *E. lecontei* as a predator by artificially infesting trees with *D. brevicomis* adults and excluding the clerids by means of cages. The final emergence of *D. brevicomis* adults in the cages was compared with that of normally infested trees to which the clerids had free access. In the cages where the clerid population was reduced to 1.5 larvae per square foot, the emergence of bark beetles was 146 per square foot; outside the cages, however, the population of clerid larvae amounted to 18 per square foot and the emergence was reduced to 52 beetles. This indicates that the clerids are capable of destroying two-thirds of the brood.

An important larval habit of E. leconteі is its tendency of moving rather freely through or over the bark and migrating when conditions become unfavorable. In 1928 Person (U235) made a study of this migration in infested trees which were felled so as to expose the top of the log to solar heat. He found that the clerids moved away from the top of the log where temperatures were sufficiently high to kill the western pine beetle and concentrated on the shaded sides and bottom of the log.

This habit suggested the possibility of building up the ratio of clerids to western pine beetle populations by falling the infested summer brood trees, leaving the bark on the log, and turning it at intervals so that most of the bark beetle broods would be killed by solar heat. This treatment, it was thought, would preserve the clerids by giving them an opportunity to migrate to the shaded sides of the log. Following up this idea, Person (U237) carried out a series of experiments during the summer of 1929 by falling infested trees and leaving the unpeeled log exposed to the sun. He found that:

> "1. Bark temperatures fatal to advanced broods of the western pine beetle are reached in unpeeled logs exposed to direct sunlight on moderately level or southerly slopes when air temperatures over 90°F. are reached; and
>
> 2. No evidence of mortality among clerids was found even when the highest bark temperatures were reached."

The following year Person (U239) continued with those experiments and uncovered further information relating to limitations of the practical application of this proposed control method. He concluded that it is applicable only to the summer period, when high temperatures prevail, and in fairly open stands where the topography is moderately level with few steep northerly exposures. An experimental project was proposed to try out the method to see if the clerid population could be proportionally increased within an area to the extent of appreciably controlling a western pine beetle infestation. This was never carried into effect, however, and the study was closed with Person's published article (106).

The red-bellied clerid, *Enoclerus sphegeus* (Fabr.).--This beetle is quite commonly predacious on *D. monticolae*, *D. ponderosae*, and other bark beetles that develop in the inner bark. Its habits are similar to the black-bellied clerid. Person (U231) notes that it is "occasionally predacious to western pine beetle adults, but never on the broods."

Miscellaneous insect predators.—

Aulonium longum Lec. (Family Colydiidae). Keen (U126) found this beetle "abundantly in *D. brevicomis* infested trees" and assumed that it was predacious. Person (U231) reported that

> "larvae have been found feeding on *D. brevicomis* larvae and pupae in a few instances, and this species may be considered occasionally predacious. However, unsuccessful attempts to get either the larvae or the adults to feed on any of the stages of *D. brevicomis*....have convinced the writer that this insect is not typically predacious, and in any case is of little importance in the natural control of the western pine beetle."

Deretaphrus oregonensis Horn. (Family Colydiidae). According to Person (U231) "This is a predacious colydiid occasionally found with *D. brevicomis* but never reported as one of its predators. Keen (61) reports it as predacious on some of the Cerambycid and Buprestid larvae."

Cucujus flavipes Fab. (Family Cucujidae) is a showy red beetle that is known to be predacious in both the larval and adult stages. It is common in recently abandoned trees, but according to Person (U231) "is seldom associated with *D. brevicomis*. It is a common enemy of termites and secondary beetles."

Platysoma punctigerum Lec. (Family Histeridae). Another feeding experiment (118) showed that this beetle would feed upon western pine beetle eggs, but the life history of this predacious beetle is not well synchronized with that of the western pine beetle which throws considerable doubt on its effectiveness as an egg predator. These studies by Struble present the only verified records of destruction of the eggs by other insects, although the presence of other small predacious beetles, diptera, and pseudoscorpions in the egg galleries has led to the suspicion that some of these may feed at times upon the eggs of the beetle.

118,

Plegaderus nitidus Horn (Family Histeridae). Struble (U283) reports that this beetle feeds during both its larval and adult stages upon the eggs of the western pine beetle. This was confirmed both by observations in the egg galleries and by feeding experiments.

Othnius umbrosus Lec. (Family Othniidae). Keen (U126) found this small grey beetle in great numbers around infested trees, and suspected it of being predacious. Person (U231) reports that it "has never been reported as feeding on *D. brevicomis*. In the larval stage it is known to be predacious on *Ips oregoni* broods."

Corticeus parallelus (Melsh).(Family Tenebrionidae). Keen (U126) reports "a few dead adult of *D. brevicomis* being eaten by these beetles." Person (U231) states that "they have never been reported as predacious on any of the stages of *D. brevicomis*." Struble (118), who worked out the biology of this species, found that "the adults as well as the larvae are phytophagus, feeding on fungi under the bark."

Aside from Coleoptera, other insects have been found preying upon the western pine beetle, although not considered important factors in control.

Formica haemorrhoidalis Emery (Hymenoptera). Keen (U126) found these large red wood ants to be a serious nuisance in experimental cages where *D. brevicomis* were emerging. "They grab the beetle with their mandibles, double under their abdomen and sting it, and then carry it away. As they are often seen running over infested trees, they probably render a great service in the control of the beetles." Person (U231) states that these red ants and also large black ants of the genus Camponotus "have frequently been known to capture *D.b.* adults and carry them away to their nests, and where abundant they may be a factor in natural control."

Raphidia oblita Hagen (Neuroptera). Person (U231) was able to get "the large larvae of this insect to feed on small *D. brevicomis* larvae, but they were not able to feed on the larger larvae. They feed naturally on small dipterous larvae beneath the bark of infested trees. It is commonly associated with *D. brevicomis* in infested trees, but apparently it is not normally predacious on this bark beetle."

Mites.— According to Rust (110) mites are important predators of bark beetle eggs. He observed their feeding habits on the eggs of *Ips oregoni* and on the basis of egg counts estimated that from 10 to 85 percent of the eggs were devoured. This varied from 52 percent mortality in the first generation to 85 percent mortality in the fifth generation, with from 10 to 25 percent in the intervening generations. Rust also observed mites feeding on the eggs of *Dendroctonus pseudotsugae*; he attributed to mites a mortality of 62.5 percent of the total eggs deposited. Rust gives the following account of the habits of mites that feed on the eggs of *Ips oregoni*.

> "Four species of mites have been found in infested ponderosa pine bark, but not all of these are predacious. Those destroying the most eggs belong to the genus *Parasitus*. As they have no wings, they are forced to depend upon their host for transportation from the old brood trees to those which are newly attacked. Just prior to bark beetle emergence, the mites fasten themselves to the adult beetles. On *Ips* they are found clinging to the concave declivity and beneath the wing covers, whereas on *Dendroctonus* beetles, which have a convex declivity, the mites are found under the abdomen and beneath the wing covers. As many as 42 mature and immature mites were found clinging to one adult of *Ips oregoni*.
>
> "Because of this means of transportation, the mites arrive at the newly attacked trees with their host and consequently start to feed just as quickly as egg laying begins. The adult female mite fastens her beak in the egg and sucks the juices. As she feeds she increases in size and when all but the egg shell has been completely consumed, she begins to lay eggs. These are laid in a group around her body and are held together by a sticky fluid. The greatest number of eggs found in any one of these groups was 60. Only a few days are required for the incubation of these eggs and upon hatching the young mites scatter beneath the bark in search of food."

While mites have not been recorded as feeding on the eggs of Dendroctonus brevicomis, it is probable that they do, as mites have been frequently observed on the adult beetles and in the egg-galleries; and it is to be expected that the role of their association with D. brevicomis is similar to that with Ips.

It has been observed that certain soft-bodied mites (Pediculoides sp.) feed on the larvae and pupae of the western pine beetle, especially when mite populations become established in rearing material. No studies seem to have been made, however, to determine the effectiveness of mites in causing mortality of D. brevicomis broods. Rust (110) refers to the relation of mites to the larval mortality of bark beetles and states that "it is possible that mites are the most important biological agent in the destruction of various species of bark beetles," but does not specifically attribute mortality of D. brevicomis larval broods to mites.

Nemic Parasites

Certain nematodes associated with the mountain pine beetle have been described by Steiner (116) and Thorne (125), but so far no studies have been reported of nemic parasites associated with the western pine beetle, although undoubtedly a number of species exist which have not as yet been recognized.

Steiner suggested that "some of the nemas may prove of value in the control of beetles by acting as disease carriers and as consumers of weak or even healthy beetles and their eggs." He described three species of nematodes associated with the mountain pine beetle and suggested that two species of the Genus *Aphelenchoides* may be true parasites, but this relationship was not fully determined. Thorne described nine more species of nemic parasites associated with the mountain pine beetle, but did not determine that any of these were primary parasites.

Fungi

A white fungus, as yet undetermined, occurring in the inner bark of infested trees, has been found to cause mortality of the young larval stages of *D. brevicomis*. It may be an important factor in natural control. In the spring of 1935 when the epidemic on the Modoc National Forest went into a decline, Salman and Bongberg (U267) reported:

> "Early in the spring of 1935, a fungus having a white mycelium was found to be abundant in the galleries of broods that had overwintered in the younger larval stages. Observations made while counting broods in bark samples revealed that a considerable portion of the brood apparently had been killed by the action of the fungus. A study of the population figures secured from periodical brood counts showed in general that in trees in which the fungus was found the mortality in larval stages was higher than the average."

A green mould also develops in the inner bark under favorable moisture conditions, and has been considered detrimental to the broods. It has been found most commonly in connection with rearing experiments in the laboratory. According to Beal (U6)

> "a green fungus, identified by Wagener as a *Pencillium* was particularly abundant in the larval galleries where the brood had failed. Whether this fungus plays a part in the death of the larvae or whether it merely finds good growing conditions on the bodies of dead larvae is not known. However, because of the general saprophytic nature of this group of fungi, it is believed to be of little importance in the death of the insects."

Bacteria

The possibility of bacterial diseases becoming a factor in the control of the western pine beetle was mentioned by Person (U231). However, no evidence has been produced to indicate that anything in the nature of a wilt disease occurs in bark beetle larvae, and this lack of evidence lends support to the assumption that bacteria are not a factor in the natural control of the western pine beetle.

Viruses

No virus infection has been found associated with the western pine beetle. According to Steinhaus (117, p. 496), "No sound well-authenticated report of a virus infection in a coleopterous insect has yet been made."

Mortality During the Flight Period

From the time the beetles leave the protection of the bark, during the flight period, [and] until they become established as parent adults in newly attacked trees, they run many chances of meeting an untimely end. Beetle mortality during the flight period is often greater than during the developmental period in the host tree. With an average of 92 beetles emerging to 25 attacking per square foot, the normal flight mortality is 73 percent even if the number of trees from one generation to the next remains the same. Frequently there may be an additional 90 percent reduction in trees or a total mortality of 97.5 percent of beetle population. Mortality during the flight period has not received much study due to the difficulty of tracing beetles after they have left a tree. Predators are known to be effective during this period, particularly certain beetles and birds. Unfavorable weather conditions and the resistance of host trees are suspected of being dominant factors.

Predators

Patterson (U211) called attention to soft-billed insect-feeding birds, such as vireos, creepers, nuthatches, fly catchers, etc. as possibly being effective feeders on bark beetles during flight, but there is little evidence to show that they actually are. While this matter has not been specifically investigated for the western pine beetle, it has been studied for the mountain pine beetle. In 1928 and 1929, Rust (U243) collected specimens of five different species of insectivorous birds during the period while the beetles were flying in a heavily infested area near Sula, Montana. From stomach examinations, he concluded that "insectivorous birds destroy many *D. monticolae* adults during their flight period." Of the five species examined, the most important were night hawks, Alpine three-toed woodpeckers, and the Rocky Mountain hairy woodpecker. Since it is not to be expected that these birds discriminate between such closely allied insects as *D. brevicomis* and *D. monticolae*, a certain number of the former are undoubtedly captured in flight in areas inhabited by night hawks and birds of similar feeding habits.

Predaceous beetles which are important in capturing western pine beetle adults when they are leaving brood trees or landing on trees to be attacked include the blue-green trogositid, _Temnochila virescens_ var. _chlorida_ (see p. 213), the black-bellied clerid, _Enoclerus lecontei_ (see p. 215), and possibly others already discussed (see p. 210). These and other predaceous insects may dispose of a large number of adult beetles during the flight period.

Unfavorable Weather Conditions

As has already been mentioned (see p. 118), unseasonable weather conditions such as high winds or heavy rains during the flight period may destroy a high percentage of beetles in flight. Since the beetles do not emerge except under favorable temperature conditions, it must be quite unusual for them to be caught in flight by sudden unseasonable weather changes.

Resistance of the Host Trees

Since the western pine beetle is unable to make successful attacks on thrifty, fast-growing host trees, a great many beetles must be lost during the flight period in an unsuccessful searching for suitable susceptible trees to attack. This subject of resistant and susceptible host trees is discussed in detail in Section IV.

INSECTS ASSOCIATED WITH THE WESTERN PINE BEETLE IN THE ATTACK UPON THE LIVING TREE

The Insect Fauna of Beetle-Killed Trees

While it has been shown by caging experiments that the western pine beetle is quite capable of killing a tree on its own initiative, without the aid of other insects, it is joined in the great majority of infested trees by other cambium feeders. These associated insects usually occupy a smaller bark area than *D. brevicomis*, but they attack the living tissues of the inner bark, sometimes in advance of the pine beetle. These associated forms may have special significance in that they either weaken the tree so that it becomes attractive to the pine beetle, or are capable of recognizing and taking advantage of a weakened condition that has already developed from other causes. In this respect the infestation of certain associated insects such as *Ips* seems to act as the fuse which lights the powder train for a more serious western pine beetle epidemic.

In addition to these insects which attack the living tissues of pines in association with D. brevicomis, there are the so-called "secondaries" that breed in the bark and dead wood, act as scavengers, or are parasitic or predaceous on other forms. The insects that live in a tree after it dies are numerous both in number of species and in populations. By maintaining two-foot square cages on the lower bole of trees killed by western pine beetle to trap emergence, Buckhorn (U40) collected 80 insect species from this limited region of the tree's bole, over a period of three years. The total insects emerging in the three years is shown in Table 2

As will be noted, most of the associated insects were Coleoptera, but the orders Hymenoptera, Diptera, Hemiptera, Lepidoptera, and others are represented by a few miscellaneous species. All of these secondary species play their part in working in and under the bark and in the decaying wood of western pine beetle infested trees, but only a few are primary in contributing to the death of the tree. The relationship between these species and D. brevicomis appears to constitute a dynamic factor in the increase and decrease of western pine beetle infestations.

Table 2 .--Insects emerging from tree cages from 1933 to 1935

Insect Species	Season 1933	Season 1934	Season 1935	Total
Coleoptera				
Scolytidae	96 sq.ft.	132 sq.ft.	120 sq.ft.	348 sq.ft.
Dendroctonus brevicomis	5,609	18,501	13,255	37,365
Ips oregoni	301	152	275	728
Ips emarginatus	709	842	204	1,755
Orthotomicus ornatus	172	1,252	465	1,889
Hylurgops subcostulatus	325	140	10	475
Trypodendron ponderosae	406	86	0	492
Gnathotrichus retusus	111	419	31	561
Xyleborus scopulorum	30	157	29	216
Pityophthorus sp. near confertus	4	-	5	9
Pityogenes carinulatus	4	3	0	7
Hylastes macer	-	14	12	26
Hylastes sp.	-	13	1	14
Dendroctonus valens	-	1	-	1
Family Total	7,671	21,580	14,287	43,538
Tenebrionidae				
Corticeus (Hypophloeus) substriatus	1,387	8,285	1,924	11,596
Hius estriatus	148	823	365	1,336
Colydiidae				
Aulonium longum	1,407	2,377	1,268	5,052
Lasconotus subcostulatus	177	184	20	381
Lasconotus complex	61	113	19	193
Rhizophagidae				
Rhizophagus sculpturatus	1,677	1,378	332	3,387
Histeridae				
Plegederus nitidus	305	1,931	387	2,623
Platysoma punctigerum	235	1,206	311	1,752
Staphlylinidae				
Phloeonomus pusillus	451	1,073	32	1,556
Nudobius pugetanus Csy.	104	412	119	635
Bolitobius intrusus	39	94	50	183
Somatium sp.	43	2	-	45
Atheta sp.	2	6	2	10
Othniidae				
Othnius lugubris	201	166	97	464

Insect Species	Season 1933	Season 1934	Season 1935	Total
Nitidulidae				
Epuraea avara	115	79	36	230
Glischrochilus cylindricus	45	98	-	143
Lathridiidae				
Corticaria sp.	109	619	14	742
Enicmus fictus	4	34	13	51
Cerambycidae				
Acanthocinus obliquus	31	2	-	33
Acanthocinus spectabilis	9	3	16	28
Curculionidae				
Cossonus ponderosae	15	6	7	28
Cossonus crenatus	-	4	22	26
Gelus californicus	10	51	55	116
Cylindrocopturus longulus	2	5	4	11
Rhyncolus oregonensis	10	27	8	45
Ostomidae				
Tenebroides sinuata	18	132	79	229
Temnochila virescens	16	29	14	59
Corticotomus caviceps	3	23	4	30
Soronia guttulata	-	2	-	2
Ostoma sp.	-	1	-	1
Melandryiidae				
Carebara californica	37	100	38	175
Melyridae				
Listrus sp.	11	11	5	27
Melachius auritus	7	6	-	13
Cryptophagidae				
Cryptophagus maximus	6	19	58	83
Salebius sexdentatus	8	14	3	25
Cleridae				
Enoclerus lecontei	9	68	9	86
Enoclerus sphegeus	1	4	3	8
Cucujidae				
Cucujus clavipes	3	14	2	19
Dermestidae				
Perimegatoma varigata	1	1	-	2

Insect Species	Season 1933	Season 1934	Season 1935	Total
Buprestidae				
Melanophila californica	-	18	1	19
Elateridae				
Elater sp.	-	4	-	4
Monotomidae				
Hesperabaenus abbreviatus	-	1	-	1
Coleoptera				
Miscellaneous spp.	-	5	-	5
Total Coleoptera	14,378	41,010	19,604	74,992
Diptera				
Medeterus aldrichii	85	87	10	182
Zabrachia polita	77	11	1	89
Lonchaea sp.	18	36	11	65
Arctiphyto gilletti	20	26	-	46
Dendrophaonia n. sp.	-	5	-	5
Sciara sp.	-	20	-	20
Pseudatrachia sp.	-	7	-	7
Diptera sp.	-	28	-	28
Total Diptera	200	220	22	442
Hymenoptera				
Myrmecine ant	16	7	5	28
Idechthis sp.	-	2	14	16
Pachycerus eccoptogastri	-	3	11	14
Meteorus hypophloei	-	2	2	4
Ascogaster sp.	-	1	-	1
Halfichells sp.	-	1	-	1
Total Hymenoptera	16	16	32	64
Hemiptera				
Lyctocoris stalii	92	236	17	345
Homoptera				
Aceratagallia californica	57	76	5	138
Chelonethida				
Pseudoscorpions	28	83	9	120
Lepidoptera				
Tinea sp.	25	22	5	52
Corrodentia				
Psocids	6	1	-	7
Total adult insects	14,802	41,664	19,694	76,160

Habits and Roles of the Associated Species

The Mountain Pine Beetle, *Dendroctonus monticolae*

Aside from its primary role as a bark beetle enemy of lodgepole pine, sugar pine, and western white pine, the mountain pine beetle also occurs in association with *D. brevicomis* in ponderosa pine. (47) Evenden, Bedard, and Struble (34) have presented the more important biological information concerning this beetle and have listed ponderosa pine as one of its hosts. However, these authors state that "in California, the beetle selects sugar pine in preference to ponderosa pine." This published circular does not discuss the association of the mountain pine beetle with *D. brevicomis* infestations.

Struble (U295) has summarized the available information on the mountain pine beetle as an associated insect of *D. brevicomis* and describes the role of the beetle as follows:

> "The mountain pine beetle occurs frequently in association with the western pine beetle in ponderosa pine. Sometimes its attacks are mixed in with western pine beetle infestations; sometimes it occurs as a fill-in species between portions of the bole which were unattacked by *D. brevicomis*. The mountain pine beetle is also often found in association with flatheads, Ips, or a combined association with all these insects. Under some conditions, it is the dominant species comprising the total infestation in a given tree. In general, the infestations of this bark beetle are regarded as of less consequence in ponderosa pine than other primary species associated with the western pine beetle."

J.W. Johnson and Salman in the series of composition studies (see pp. 284) found that the role of the mountain pine beetle in mixed infestations with D. brevicomis was largely secondary. Struble compared the composition records from eastside and westside pine types and found some striking differences in behavior of D. monticolae. In the eastside pine type, 19 percent of 278 trees analyzed contained mountain pine beetle infestations which occurred mainly in the bark near the basal part of the bole; in contrast, the records from westside type showed that 65 percent of 100 trees analyzed contained mountain pine beetle infestations which occurred mainly in bark of the mid-bole. These differences in behavior between eastside and westside areas are not easily explained. Struble (U199) suggests that the greater incidence of the beetle in the westside stands is "the result of a much closer association with sugar pine which is the preferred host of the mountain pine beetle." This means that centers of attack which form in sugar pine may sometimes include nearby ponderosa pine. It may also mean that the moister westside conditions are more favorable for this beetle's development than the more arid eastside.

The Red Turpentine Beetle, *Dendroctonus valens* Lec.

The red turpentine beetle is probably the most common species of bark beetle found attacking practically all species of pine and spruce throughout North America. Hopkins recognized its common role and preferences when he stated (43,p156):

> "This species prefers to enter the bark of injured or dying trees or that of stumps and logs of those which have been felled, but often attacks the perfectly healthy bark on the base and roots of healthy, living trees.---It is often exceedingly abundant in the stumps of felled trees where timber-cutting operations are carried on, in fire-scorched trees, and especially in the bark at the base of those killed by other species of *Dendroctonus*, or by lightning or storm, or otherwise injured and broken. It shows a decided preference for the bark on the base of pine trees and stumps, and is rarely common in the logs or prostrate trunks, even of pine."

Its attacks on standing trees seldom are found more than 6 feet above the root collar, but may extend down the main roots for 15 feet or more.

That this species is strongly attracted to stumps on recently cutover areas, and to injured or weakened trees, is well established. Bongberg (U25) found them attacking stumps and an occasional green tree along with freshly cut stumps on the Black's Mountain experimental cuttings, and Johnson (U113) found that "the only attacks on standing trees in cutover areas were on trees either injured by logging or those close to stumps or green logs," which provided a strong attractive influence. Johnson also summarized the previous work on this beetle in addition to adding his own field data.

This beetle has rarely been regarded as a primary tree-killing species in ponderosa pine, but whether it is one of the first to attack and weaken trees or merely follows behind the attack of other species has been a subject of some uncertainty. Struble (U282) in studying this species in relation to other species associated with the western pine beetle on the Sierra National Forest in 1927, concluded that "*D. valens* is a secondary insect and is rarely able to make successful attacks until the tree has been overcome by some other agency." He believed that the scent of fresh pitch tubes of the other species was influential in attracting *D. valens* to the attacked trees. When in association with *D. brevicomis*, *Ips confusus*, *D. monticolae*, and Buprestids, *D. valens* in the most cases had the youngest broods indicating that it was the last or nearly the last insect to attack the trees.

On the other hand, in field studies in eastern Oregon, Keen found that there was a definite tendency for *D. valens* to initiate attacks on very high risk trees, and that such trees were four times as susceptible to subsequent attack by *D. brevicomis* as the average tree in the stand. Johnson (U114) found it attacking both high and low risk trees at Black's Mountain Experimental Forest, sometimes following attacks by *Melanophila*, *D. brevicomis*, or *D. monticolae*, but in a few cases apparently attacking before any other insects.

Often D. valens attempts to attack apparently vigorous green trees, but if it is not supported by other insects attacking up the main bole, it is usually drowned out by pitch flow, fails to develop successful broods, and such trees survive. But repeated attacks by D. valens may weaken trees to the point where they become susceptible to other bark beetles.

Callaham (U46) studied this species in the Jeffrey pine stands of the Laguna recreational area in southern California and found D. valens and Melanophila californica to be the most common initial insects in dying trees and strongly associated with stand decadence. But he was unable to determine whether these species attacked because of tree decadence or were actually responsible for tree decline.

The evidence so far strongly supports the conclusion that D. valens is a secondary species which prefers stumps, injured, weakened, or decadent trees. In ponderosa pine it usually follows other Dendroctonus or Melanophila californica by attacking and filling in the base and roots of killed trees. But frequently it attacks fire-injured, drought-weakened, or decadent pines before other species do, and by its work at the base renders such trees more susceptible to them. It is doubtful if it can attack and kill a fully vigorous, healthy tree, without assistance from other primary species.

Brood development is slow, with a single generation a year indicated for northern California (U114), one and a partial second generation in the southern Sierras (U282), and probably two generations a year in the San Francisco bay area (130).

The red turpentine beetle, D. valens can be controlled in park and shade trees by injecting orthodichlorobenzene, ethylene dichloride, or carbon disulphide into the tunnels (U246) or by cutting out the galleries of the beetle with a chisel and then coating the exposed wood with pruning paint (28).

The Oregon Pine Engraver Beetle, Ips oregoni Eichh.

This insect is quite commonly associated with the western pine beetle in the interior ponderosa pine type. While it breeds with the western pine beetle in windfalls, and occasionally in large standing trees, it more commonly works alone, killing large patches of reproductions, trees of pole size, or the tops of older ones. Usually it attacks where the bark is thin, either on small trees, the tops of larger ones, or on the larger limbs. This attack may either precede or follow the attack of D. brevicomis on the main bole, and often represent a small portion of the infestation found in the tops of western pine beetle infested trees and poles, or be quite independent of it. Its egg galleries may also occur in mixture with D. brevicomis in the upper half of the bole under thicker bark. While a very considerable amount of unpublished information concerning this species has accumulated in manuscript and progress reports, there is almost a total lack of published information on this species.

Outbreaks of Ips oregoni have almost invariably followed windfalls (86, 131); logging disturbance (U133, U191, U10, U42); and slash due to road construction or pine thinnings (U60, U225, U1, U2); and drought years (U88).

Keen (U130) studied the seasonal history and habits of this species in the Ashland area of southern Oregon and reported 54 days from first attack on April 10 to first emergence on June 3. While the generations were not closely followed, they indicated "one summer generation in newly felled logs, and an overwintering generation in the tops of mature or young trees."

Rust (U247), who studied the species intensively for three seasons in Idaho, found four generations produced annually with a fifth generation produced in the exceptionally long season of 1931. In the Black Hills of South Dakota, Baumhofer and Hauke (U2) found three generations with only two and a partial third generation produced in some years.

Buckhorn (U42) found that the main attack on slash in eastern Oregon usually occurred about the middle of April with heavy emergence from slash occurring about the middle of June. General attack on reproduction and standing trees started early in July and continued during August and September. Rust found a minimum time of attack to emergence of 24 days, but the usual time required was from 30 to 66 days.

One peculiarity of this beetle is the habit of the adults to congregate under the bark of small trees late in the summer and fall where they feed on the inner phloem and reduce it to powder. Another striking habit is that of the adults to overwinter in great numbers in bark crevices at the base of trees, in the forest duff, and in egg galleries of *D. brevicomis*. Keen's note (66) was the first published information on this hibernating habit. The extent to which *Ips* populations overwinter in this way was effectively demonstrated by caging experiments conducted by Buckhorn (U38,U39,40) in eastern Oregon.

While it is present every year, its outbreaks occur in certain "*Ips* years," and, as shown by Buckhorn (U42), these seem to be tied in to precipitation deficiencies. These outbreaks are sporadic in occurrence, and usually take smaller size trees than are attractive to the western pine beetle. Therefore, its association with *D. brevicomis* is usually of minor importance.

The California Five-Spined Engraver Beetle, Ips confusus Lec.

Some of the earliest work in California was concerned with the habits, seasonal history, and control of this species. The first observations were made by H.E. Burke in the vicinity of Pyramid Ranger Station, above Placerville, California, in 1906. Over the years since then, intermittent studies and notes by a number of forest entomologists have accumulated considerable information on this species. Those who made special studies include Keen (U123) at Ashland, Oregon; Herbert (U94) at Placerville, California; Miller (U173) on the Kaweah River; Furniss (U62) near North Fork, California; and Salman (U263) in connection with the composition studies. In 1945, Miller (U200) summarized the notes and reports on this species in the Berkeley files. Further work was undertaken on the biology, ecology, and control of this species from 1946 to 1950 by G.R. Struble (U298,U299, U300,U301,U302); R.C. Hall,(U83,U84,U85 terson);and J.E. Patterson (U221). This work, together with information derived from earlier studies, is being prepared for publication by Struble and Hall. (U303).

In the collections made by Berkeley Laboratory workers ten native species of pine have been recorded as hosts of *Ips confusus*. These include *Pinus attenuata*, *P. balfouriana*, *P. coulteri*, *P. jeffreyi*, *P. lambertiana*, *P. monophylla*, *P. monticola*, *P. ponderosa*, *P. radiata*, and *P. sabiniana*. But out of the 158 note entries, 114 apply to ponderosa pine, which is obviously one of the preferred hosts. The notes show the species distributed through the westside pine types all the way from the Rogue River in Oregon, to the Laguna Mountains in San Diego County, California. It is significant that in these notes there is no record of *Ips confusus* from any areas east of the Cascade Mountains or the northern Sierra Nevadas. However, it appears in pinyon pine (*Pinus monophylla*) east of the southern Sierras from Mommoth Pass south to the Mexican border and in the Sierra Madre Mountains of southern California.

Some interesting observations on the apparent introduction of this species into a new area was published by R.W. Doane (29). He found it in Monterey pine near Palo Alto, California, for the first time in 1921. Formerly *Ips* infestations in this area had consisted of *I. plastographus* and *I radiatae*. *I. confusus* was apparently brought in with slabs of ponderosa pine wood. Following its introduction it spread rapidly and became the dominant species, crowding out both of the former species in dying trees. Doane offered as an explanation that "*Ips confusus* is able to maintain itself in trees that would repel either of the other two species."

The biology, seasonal history, and habits can be broadly sketched from the available information. All reports on the subject agree that for the most part, broods carry through the winter in standing trees attacked the preceding fall, and that these broods are made up mainly of new adults with some advanced larvae and pupae. The development of generations through the active season depends upon latitude and elevation, and may vary from two to three and a partial fourth. Miller (U200) summarizes these as follows:

> "Emergence of the overwintering generation begins early in March at the lower elevations (Placerville records) and continues through April and May (North Fork records).
>
> "Attacks of the first seasonal generation begin about March (Placerville), continue during April (Ashland), the early part of May (Bass Lake), and may even occur as late as early June at the higher elevations (Kaweah area). These attacks are most common in windfalls and slash material when this is available. Development of this generation is completed in from 45 days (Bass Lake and Kaweah) to 86 days (Ashland); the length of this period is undoubtedly influenced by elevation and seasonal temperatures. Emergence begins about the middle or last of June (Placerville and Bass Lake) and may occur as late as the latter part of July or early August (Ashland).
>
> "A second seasonal generation occurs in traps at lower elevations from the middle of June to the latter part of July (Bass Lake). This generation may complete development from attack to emergence in 35 days.

> "A third seasonal generation in the lower pine belt occurs in traps from the first part of August to the last of September and emerges before winter (Bass Lake). Under normal conditions, it can be expected that this generation attacks mainly in standing trees, but brood records have been obtained only from trap material.
>
> "A partial fourth generation can be expected which attacks in late September and October and establishes the overwintering broods in the lower pine belt, although this has not been shown by available records."

The behavior of *Ips confusus* infestations appears to be quite similar to *Ips oregoni*. Under endemic conditions both *Ips* maintain themselves in recently felled logs, tops, and limbs. These infestations may be followed by localized attacks on nearby standing green trees. But when outbreaks of *Ips confusus* occur, a somewhat larger class of poles and young trees are attacked and killed. An immense amount of damage may rapidly occur over large areas. These extensive outbreaks have usually been short lived, and often are associated with or followed by *D. brevicomis* which breeds in the green boles of the top-killed trees and carries on the momentum of the epidemic for several years even after the *Ips* have subsided.

Outbreaks seem to occur over a large part of its range in certain "*Ips* years." Important epidemics which have been recorded include the Sierra National Forest, 1912-13; Placerville, 1914-16; Ashland, Oregon area, 1915-16; west slope of the Sierras, 1929-32; northern California, 1938; (U276) the Burney and west slope Sierra areas, in 1944-45. In southern California outbreaks have occurred every few years ever since observations were first made by Keen on the Julian area in 1915. The latest outbreaks started on this area in 1945, and were reported by Engen (U55,U56).

The actual tie-in of western pine beetle epidemics to preliminary outbreaks of *Ips* was not very well established in early records. It was generally recognized from observations that some of the earlier western pine beetle epidemics (pages 293, 302) were preceded by widespread tree-killing and top-killing by *Ips* before the western pine beetle became the dominant insect in the total infestation. This applies especially to the Rogue River (1914-1917), and the westside Sierra (1912-1917 and 1929-1933). Further data on these earlier infestations are presented in topic on composition types (Section III, pages 279-284) The areas where this *Ips*.-*D. brevicomis* sequence occurred were all in the westside pine types where *Ips confusus* was the species concerned. There is no evidence of a similar sequence in the eastside pine types where *Ips oregoni* is involved.

In the outbreaks that occurred during the 1943-1949 period, studies were concentrated on the biology and ecology of Ips, and no special effort was made in a quantitative way, to show the build-up of D. brevicomis following Ips infestations. However, some evidence was obtained, which is presented in table 3 .

Table 3 --Follow-up of western pine beetle in recent *Ips* outbreaks.

Name of area	Ratio of *Ips* to *D. brevicomis* in Total Population		
	During origin of outbreak	Following outbreak	
Burney area	General outbreak started in 1943 and continued in 1944. Composed of: *Ips*- approx. 75% *D.b.*- approx. 25% Control-Spring,1945	Season of 1945 Total infestation greatly reduced. Composed of: *Ips* - 20% *D.b.*- 80% Control-Spring 1946	Season of 1946 Endemic infestations, some local outbreaks *Ips* - 10% *D.b.*- 90%
Cobb Mt.	Heavy general outbreak in fall, 1948 *Ips* - 90% *D.b.*- 10% Control-Spring,1949	Season of 1949 Spring period *Ips* bred up in snowbreak and attacked living trees *Ips* - 90% *D.b.*- 10%	Late fall period heavy infestation in large trees *Ips* - 50% *D.b.*- 50%
Sierra areas (Mariposa and King's River)	Heavy *Ips* outbreaks around cutting areas during season of 1947 *Ips* - 90% *D.b.*- 10% No control	Season of 1948 Infestation greatly reduced. Composed of: *Ips* - 80% *D.b.*- 20%	Season of 1949 Epidemic conditions *Ips* - 10% *D.b.*-90%
Julian and Cuyamaca areas southern California	*Ips* outbreak started in 1945, discovered in 1946, control in 1947-48 *Ips* - 90% *D.b.* -10%	Season of 1948 Epidemic reduced Control continued *Ips* - 70% *D.b.* -30%	Season of 1949 *Ips* epidemic greatly reduced. *D.b.* population increasing *Ips* - 10% *D.b.*- 90%

The ratio of Ips to D. brevicomis in the areas included in this list is expressed only on an estimate basis and is therefore subject to limitations, but it serves to show the change from Ips to a predominantly D. brevicomis population in each area.

In the Burney area no serious epidemic of D. brevicomis occurred, but in the endemic infestation that followed the outbreak, the western pine beetle became the dominant insect.

In the Cobb Mountain area there was an apparent reversal of the Ips-D. brevicomis ratio in mid-season during the first year after the outbreak. In the Sierra area the western pine beetle apparently required two seasons to reach its full momentum, while at Julian it required four seasons.

There is no evidence that control work or natural control factors against Ips had much effect in preventing the build-up of D. brevicomis populations.

Epidemics of Ips have been attributed to varied causes. It has usually been assumed by nearly all observers that the attacks in groups of standing green poles and the tops of living trees came from increasing Ips populations which had first gained momentum by breeding in tops and logs of freshly felled trees, or injured and dying standing trees. Conditions considered as contributing causes for Ips outbreaks have included windfalls, snowbreak, slash created by wood cutting, logging operations, thinnings, road and reservoir development, flooding of pole stands, drought, suppression of tree growth, and the effects of fire injury. While certain of these conditions seem to have afforded plausible explanations for specific outbreaks, no case can be said to have been conclusively proven. It is fairly apparent that there are a number of factors involved in every situation which has preceded an outbreak of Ips confusus. Of these factors, Hall and others have given especial attention to the influence of precipitation and temperature in studies since 1945.

Precipitation.— Precipitation deficiencies were found to be associated with both recent and older epidemics of Ips in California. Hall (U85) reviewed the known history and the available precipitation records of 12 different Ips epidemics extending from Ashland, Oregon, to Julian, California. He found that for most of these outbreaks, there had been precipitation deficiencies during the late winter and spring periods which preceded attacks in living trees during the late summer and fall. The precipitation pattern arrived at by plotting the arithmetical accumulation of departure from the monthly means developed a certain character by the early part of May, after which there was little change from the seasonal trend. When there was a cumulative deficiency in these areas from January to June which reached a point as low as 75 percent of normal, Ips outbreaks usually occurred in the late summer and fall. Conversely, above normal precipitation during this period, usually coincided with very low or negligible damage by Ips during the late season. In the Burney area soil moisture was found to follow the precipitation trend and showed pretty much the same relationship to Ips damage.

Temperature.— In northern California, Hall (U84) reported marked differences between the seasons of 1947 and 1948 in the intensity of Ips infestations, and attributed these differences to variations in precipitation and temperatures.

The year 1947 was one of heavy Ips damage in the lower westside pine types. This season was characterized by seasonal precipitation well below normal, soil moisture well below normal during most of the growing season, and by air temperatures well above normal during most of the growing season.

The season of 1948 was one of very light Ips damage except for a few local areas. This season was characterized by seasonal precipitation and soil moisture well above normal for the entire growing season and by air temperatures below normal through most of the season.

It was estimated that the low air temperatures in 1948 slowed down the development of Ips broods to the extent that only 2½ generations were produced that season as compared with 3½ generations in 1947.

In the central Sierra region, Struble (U301) found practically the same differences in number of generations between these two seasons. In the Julian area in southern California, however, Engen (U56) recorded prolonged seasonal activity in 1948. He estimated that four complete generations and a partial fifth were completed between April 14 and November 15. Some attacks of the first generation were noted in January and February 1948 but the brood development of these early attacks was very slow because of low temperatures prior to April.

Differences in responses of Ips and D. brevicomis to climatic influences.— In the over-all effects of precipitation and temperatures, all investigators agree that a combination of sub-normal seasonal precipitation and soil moisture, and air temperatures above normal during the growing period, sets up conditions highly favorable to Ips activity and the prospect for outbreaks in living pine stands.

Western pine beetle populations apparently respond in the same way to precipitation deficiencies (see Section IV, pages 396-398) and to above normal seasonal temperatures (Section IV, page 402) but at a much slower rate. It was shown that D. brevicomis epidemics correlate very well with cumulative deficiencies in precipitation extending over more than one season, while Ips outbreaks usually appear during the first season of drought. This point may explain the lag of western pine beetle populations behind increasing Ips populations.

Practically all epidemics have reached their peak in one or two seasons and have subsided as suddenly as they developed. The causes for the sudden disappearance of Ips populations, once they have reached their peak, are as difficult to find as the causes for their rapid increase. So far only two explanations have been offered for specific cases - "lack of wind-blown material or other suitable material for the development of the first seasonal generation" (U123); and, in the case of the sudden decline in 1932, failure (from unknown causes) of overwintering broods to develop successfully in top-killed trees in the fall of 1931, so that not enough beetles emerged in the spring of 1932 to maintain the momentum of the infestation (U62). While the ecological factors favorable to an increase in Ips populations appear to be also favorable to western pine beetle increases, the natural control factors which bring about sudden declines in Ips populations do not appear to work so rapidly on western pine beetle epidemics, and these may proceed to increase, after the Ips outbreak has passed out of existence.

Direct control.-- Direct control of Ips confusus, like the control of Ips oregoni, has largely been considered incidental to the control of the western pine beetle in commercial pine stands. The policy seems to have been based on the expectation that the Ips infestation would die down quickly and that the important thing was [the] to prevent the build-up of D. brevicomis populations in trees that had been injured by Ips top-killing. Miller (U200) states that:

> "The general policy regarding Ips on all direct control projects since 1920 has been to treat this infestation only when it could be included with the treatment of D. brevicomis and D. monticolae infestations, except on parks, recreational areas and other conditions where the character of the damage caused by Ips was considered to be a serious threat to tree cover values; in the latter case, the effort has been made to eradicate all Ips infestation in the control area."

Direct control methods have consisted mainly of the cut-peel-burn technique, or in the case of pole groupings, cutting and burning the trees in piles without peeling.

Indirect control has been considered by forest management agencies through measures to prevent the slash conditions that provide breeding grounds for Ips populations. This has taken the form of specific requirements for slash disposal on sporadic cuttings, such as right-of-way clearings and other operations that create a considerable concentration of slash for a short period. Continuous logging operations have usually been excluded from any special disposal requirements because it was assumed that the constant supply of fresh slash under continued logging provided ample material to absorb surplus Ips populations.

The Large Western Pine Engraver, *Ips emarginatus* Lec.

Although *Ips emarginatus* is a common associated insect, very little work has been done on its [the] biology. [of *Ips emarginatus* Lec.] The first observations were made by Keen (U130) on the Ashland area in 1916. He found that "there are at least two generations, one developing during the summer and another passing through the winter." Flight and new attacks were observed in May and June and again in August and September. The species overwinters as adults, eggs, and small larvae.

According to Salman (U263), *Ips emarginatus* is of relatively minor importance, usually occurring in association with other species and often following after them, filling in its attacks in patches and strips on the middle and lower bole left by other beetles. During 1933 on the Lassen National Forest, Salman found this species competing with the western pine beetle by following in, cleaning out, and widening the western pine beetle galleries. Many of the younger stages of western pine beetle broods were thus destroyed.

It is often associated with *Dendroctonus monticolae* in ponderosa pines of small diameter, but is definitely a secondary species. Apparently it never becomes aggressive or is found attacking and killing tops or young trees as is the case with *Ips oregoni* and *I. confusus*.

The Flatheaded Borers, Buprestidae.

Although some of the flatheaded borers are cambium feeders, these insects are strikingly different from the scolytids in their habits of attack and development. Eggs are laid in crevices of the bark and only the larvae penetrate into the phloem area and later into the wood, where they make flat tortucous mines packed with concentric layers of frass. Pupation occurs in cells in bark or wood.

The species most frequently found in the bark of ponderosa pine associated with the western pine beetle are *Melanophila gentilis* Lec. and *M. californica* VanD.

Melanophila gentilis Lec.-- The adults of this species are bluish-green in color and 13 mm. long. Burke (14) records this species as mining the bark and outer wood of normal, injured, dying, and dead ponderosa pine, Jeffrey pines, and sugar pines throughout the Pacific States and Rocky Mountain region. Keen (U130) noted flatheads killing trees on the Ashland area from 1915 to 1917, but kept no consecutive records of their development. The species was considered to be *M. gentilis*, and those attacking logs probably were, but the species found in standing trees was probably *M. californica*, which was not described by Van Dyke until 1918.

From the more intensive work of Salman (U263), Salman and Bongberg (U269) it was determined that "M. gentilis appears to be the species chiefly concerned in infestations of felled trees, logs, windfalls, injured trees and in secondary bole infestations in standing trees." The more primary infestation in standing trees was due to M. californica.

West (U320) confirmed this appraisal of the secondary rôle of M. gentilis. He found that in common with M. californica the adults of M. gentilis emerge and have an extended flight period in the late spring, during which they feed on pine foliage before they become sexually mature. Eggs are deposited on the outer bark and the young larvae feed in the cambium and inner bark. However, from this point on there were significant differences in habits of the two species. West found that M. gentilis developed only in felled green trees, windfalls, phloem of infested trees, cull logs, and slash, and completed its life cycle in one year. This was in contrast to M. californica which completed its development only when the young larvae spent at least one season in the living phloem and cambium and usually required from two to four years to complete the life cycle. West concluded, therefore, that the secondary importance of M. gentilis had been established to the point of dropping the species from serious consideration as an important factor in association with western pine beetle attack.

Melanophila californica Van Dyke.-- The adults are brownish-black on the dorsal surface, and greenish bronze below. Some specimens have two to six yellow spots on the wing covers. The length is from 7 to 11 mm. This species was not recognized until 1918 when Van Dyke separated it from M. drummondi and its other near relatives.

Burke (14) reported it mining the inner bark and outer wood of normal, injured, dying and dead ponderosa pine, Jeffrey pine, digger pine, Coulter pine, Monterey and knobcome pine in California, Oregon, and Idaho.

In 1935, Salman (U263) found from composition studies that Melanophila californica and not M. gentilis was responsible for the greater portion of the flathead infestation, particularly in eastside stands, where in some areas and seasons the flathead damage was nearly equal in amount to that caused by the western pine beetle. In westside stands, flathead infestation was usually confined to smaller trees growing on poor sites and topkilling, particularly in the follow up of top damage by Ips confusus.

The composition studies further showed that on the eastside, the attack by this species frequently occurred in the tops of slow-growing trees and that this attack was usually followed by that of the western pine beetle. It was assumed, therefore, that this initial attack by this flatheaded borer was a primary factor in weakening trees and in producing those characters associated with high risk to pine beetle attack. This led to a series of studies on the biology and role of this flatheaded borer in eastside pine stands.

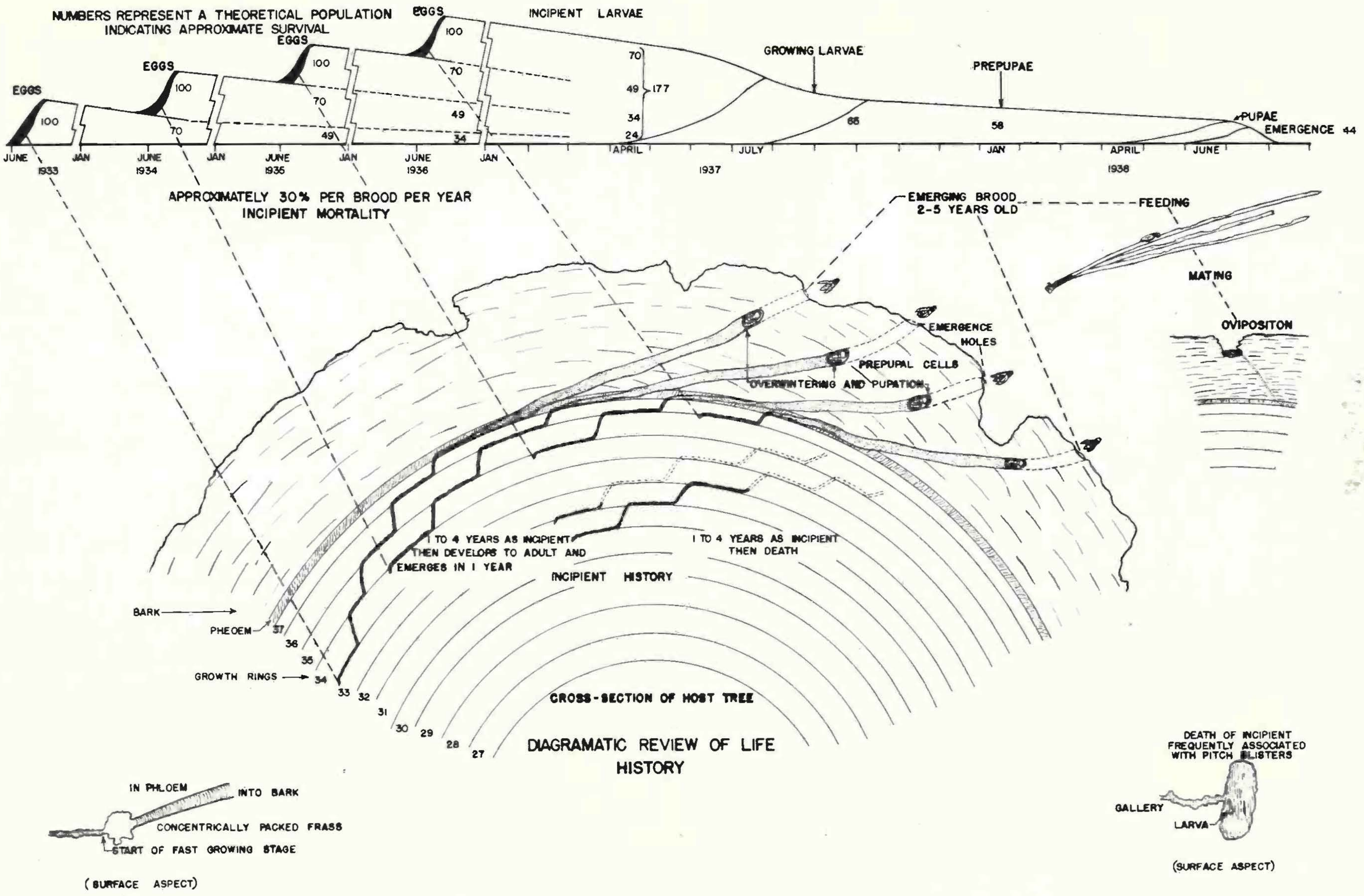
In the life history studies, West (135;U320) found that the adults of *M. californica* emerged during May, June, and July, and only became sexually mature after feeding on the needles of ponderosa or Jeffrey pine. They then laid eggs during June, July, and August on the outer bark of living trees. Upon hatching, the larvae worked into the cambium area and began feeding. These first larval mines were associated with wart-like scars formed by wood tissues laid down over the feeding injury. This peculiar phase of feeding in which the tree continued to grow and the larva very slowly increased in size and widened its mine was termed the *incipient stage*. It was found to persist from one to four years depending on how long the tree continued to live and form scar tissues around the mine.

Once the tree ceased growing, the larvae passed into the *fast growing stage*, in which it began feeding rapidly in the inner bark, completed its development, and pupated in the outer bark. This fast growing period was usually completed within the same season that the larvae changed over from the incipient stage. As a rule the fast growing stage overwintered as prepupal larvae in the outer bark and the following spring transformed to the new adults and emerged. A diagram of the seasonal and life history of *M. californica*, as worked out by West, is shown by Figure 23.

Figure 23.--Life cycle of a typical *Melanophila californica*, mixed aged brood.

(Page 261a follows)

Figure 23.-- Life cycle of a typical *Melanophila californica*,


NUMBERS REPRESENT A THEORETICAL POPULATION
INDICATING APPROXIMATE SURVIVAL
EGGS
100
EGGS
100
70
EGGS
100
70
49
EGGS
100
70
49
34
EGGS
100
70
49
34
24
INCIPIENT LARVAE
70
49
34
24
177
GROWING LARVAE
68
PREPUPAE
58
PUPAE
EMERGENCE 44
JUNE
1933
JAN
JUNE
1934
JAN
JUNE
1935
JAN
JUNE
1936
JAN
APRIL
JULY
1937
JAN
APRIL
JUNE
1938
APPROXIMATELY 30% PER BROOD PER YEAR
INCIPIENT MORTALITY
EMERGING BROOD
2-5 YEARS OLD
FEEDING
MATING
OVIPOSITON
EMERGENCE
HOLES
PREPUPAL CELLS
OVERWINTERING AND PUPATION
1 TO 4 YEARS AS INCIPIENT
THEN DEVELOPS TO ADULT AND
EMERGES IN 1 YEAR
1 TO 4 YEARS AS INCIPIENT
THEN DEATH
INCIPIENT HISTORY
BARK
PHEOEM
37
36
35
GROWTH RINGS
34
33
32
31
30
29
28
27
CROSS-SECTION OF HOST TREE
DIAGRAMATIC REVIEW OF LIFE
HISTORY
DEATH OF INCIPIENT
FREQUENTLY ASSOCIATED
WITH PITCH BLISTERS
GALLERY
LARVA
(SURFACE ASPECT)
IN PHLOEM
INTO BARK
CONCENTRICALLY PACKED FRASS
START OF FAST GROWING STAGE
(SURFACE ASPECT)

During the 1936 season, West (U313) made a very thorough investigation of the biology of M. californica. A field laboratory with insectary and rearing cages on the Modoc National Forest was utilized to study all phases of the insect's behavior under control. The more significant points established by the work of this season were:

> "Needle feeding is a requisite of adult life.
>
> "Attempted forced attacks on green logs were definitely unsuccessful.
>
> "The life cycle of M. californica in northern California is generally longer than one year.
>
> "The length of time spent in the incipient larval stage depends on the condition of the host.
>
> "Many trees bear evidence of continued unsuccessful incipient attacks.
>
> "The growth from the incipient to the prepupal stage is very rapid.
>
> "In mixed stands of ponderosa and Jeffrey pine, the latter is apparently the preferred host."

West (U312) ran a short series of laboratory tests at Berkeley to determine the cold resistance of Melanophila larvae. These indicated appreciable mortality after several days' exposure between + 14 and 0, with increasing mortality from 0 to -15° F. West pointed out, however, that these results did not apply to field conditions since the larvae used in the tests did not undergo the hardening process of fall weather.

West (U315) continued these studies during the 1937 season and added somewhat to the knowledge of the species as well as verifying the results of previous studies. The prolongation of the incipient stage was definitely established to last from one to four years. West found that

> "the life cycle for the greater part of an emerging brood has been 2 or more years. Larval studies have shown that as many as 4 distinct ages of incipient larvae may be present in the same section of an infested bole, with the proportion of larvae of any one age to the total brood varying inversely with the age of the group... The physiological condition of the host determines the time when larvae leave the incipient stage to complete their development."

That a period of feeding in living cambium is a requirement for successful development of M. californica larvae and that this habit requires a life cycle of at least two years were established by West and are specific differences between the habits of this species and M. gentilis. A paper summarizing these studies was published by West in 1947 (135).

In 1941 J.W. Johnson (U108) carried out a study to recheck the points established by West's studies. Johnson found that "at times small larvae of the season may be able to develop into the fast growing condition and possibly to maturity without having spent a year in the green trees as incipients." The data supporting this, however, were limited to one, or possibly two, trees out of many that have been studied. Johnson also investigated the possibility that incipient larvae may go into the fast growing stage, pupate, and change to adults in the same season without overwintering as mature larvae, but concluded that "it may be possible that development from incipient to the adult can occur within a single growing season, although the data are inconclusive for this possibility." Johnson (U112) also found that in some atypical cases, emergence from the same piece of bark may occur during two seasons. However, such split emergence seems to be of infrequent occurrence.

Rust (U248) also carried on some rearing experiments at Coeur d'Alene, Idaho, 1939-1942, which indicated the possibility that M. californica may complete its life cycle in one year and that it may develop successfully in slash. However, the conditions of the experiment were such that these results were not conclusive.

The capacity of M. californica to weaken trees and make them attractive to western pine beetle attack was considered to be due to the injury caused by the incipient mines in the cambium. West (U314) first went into a careful histological study of the nature of these mines to determine the type of injury they produce and their effect upon growth of the tree. He found that the healing over of the lesion produced by the larval mine was accompanied by the formation of considerable abnormal tissue and that resins infiltrated much of the tissue surrounding the scar.

It was suspected that this abnormal tissue and the resins could affect the tree's functions adversely by blocking conduction. To determine this point, Salman and Johnson (U277) made a detailed study of the movement of water through and around the scars produced by incipient larval mines in living trees. Special staining technique was developed which brought out the rate of flow of silver nitrate solutions through the different wood layers. The wood material used was collected from living trees and immediately subjected to injection of the solution through gravity pressure. It was found that the outer wood rings conducted the solution most readily, but that this movement was retarded when flathead scars were present. The conclusions stated were that

> "flathead scars seem to have a definite blocking effect upon solutions moving dynamically through scarred wood. This effect results in a reduction in the amount of wood available for rapid transport of the staining solution longitudinally through the wood. If the results of this study are applicable to living trees, the flathead scars may exercise a definite influence upon the tree by affecting the water relations."

Salman (U279) explored the effect of incipient scars upon the growth rate and the relation of these scars to risk in ponderosa pine on the Modoc National Forest. A series of typical trees were used to illustrate the crown characters indicative of risk and the corresponding growth patterns of these trees, together with the relative abundance of incipient mines. Salman reached the following conclusions:

> "The types of trees in which most of the loss has been recorded, i.e. high risk trees, are generally the slower growing ones.
>
> "The slow growth rate is of recent origin and probably temporary, to be terminated by death or recovery.
>
> "Incipient infestations tended to occur more often in the trees which subsequently died than they did in the stand as a whole."

Salman's data also showed that incipient infestations preceded death in 80 percent of the trees that were attacked by the western pine beetle. His results indicated that for this particular area the association of _M. californica_ with _D. brevicomis_ was practically universal and that the presence of incipient larval mines is associated with, if not the cause of, recent suppression of growth rate.

Twig Beetles, _Pityophthorus_ and _Pityogenes_

Other beetles that at times appear to be associated with western pine beetle attack are the tiny scolytids that breed in the thin bark of the extreme top, limbs, and twigs.

The most common species in this type of association belong to the genus _Pityophthorus_. Their activity is associated with the killing of the upper two to ten feet of the crown. In some cases this is followed by the attack of _Ips_ and _D. brevicomis_ on the main bole; more often, however, no subsequent attack develops and the tree survives with a small dead spike in the top. Because of the limited character of the attack, this type of injury has been termed "tip killing." It is quite sporadic in its behavior, developing suddenly over wide areas one season and disappearing the next.

In 1935 and 1936, Salman (113) made a study of a tip-killing epidemic which was prevalent in several forested areas in northern California. He noted:

> "The *Pityophthorus* infestations were widespread and occurred in markedly different environments. They were present in stands of varied composition, character, and general vigor. They were found in both virgin and cutover stands. The thriftiest trees seemed to be selected for infestation to a greater degree than the less thrifty trees."

In the absence of any other evident primary cause he attributed the damage to two species of *Pityophthorus*, *P. confinis* Lec. and *P. confertus* Sw. though these insects had not previously been known to cause such damage. However, he stated, "it is possible that the trees had previously been weakened and their resistance to insect attack reduced by some other environmental factor. If such was the case, that factor could not be determined."

Wagener (128) showed that top dying of Coulter pine on an area in southern California was due to freezing injury when a sudden cold spell followed a period of warm weather which had rendered the inner bark sensitive, and that top dying on ponderosa pines in northern California was probably due to the same cause. He stated:

> "Similar freezing injury has been found in connection with top dying of ponderosa pine in northern California and may have been the primary cause for earlier top kill in this species ascribed to *Pityophthorus* beetles. Freezing is to be suspected as a cause when top dying appears early in the season and is confined to fully exposed tops of thrifty trees."

It has been found in general that *D. brevicomis* followed only when the tip killing included more than the upper few feet of the top and was associated with some *Ips* infestation.

Pityogenes carinulatus Lec. is sometimes found in western pine beetle infested trees. This scolytid attacks the lateral small branches and twigs of dying pines. No studies have been made of this association, but the available records indicate that it is entirely secondary and is in all probability attracted to the tree after the attackby *D. brevicomis* or some other agency responsible for the dying condition.

Defoliating Insects

Insects which feed on the needles and thus defoliate pines may contribute to an attack of *D. brevicomis*. If defoliation is severe and rather sudden, the tendency is to stop transpiration and cause an accumulation of moisture or "sour-sap" condition in the sapwood and phloem which is decidedly unfavorable to bark beetle attack (see page 165). This effect has been noted in the case of sudden defoliation by fire, needle-cast fungus, or defoliating insects. On the other hand, a slower, more progressive type of defoliation may cause a gradual suppression of growth and tree vigor which will make trees susceptible to *D. brevicomis* attack. Two important pine foliage feeding insects have been studied in their relation to western pine beetle outbreaks and deserve mention.

On June 6, 1899, Dr. A.D. Hopkins found D. brevicomis "in the bark of pine trees which had been defoliated the previous year by the caterpillars of the pine butterfly (Neophasia menapia Feld.)." He found also that this beetle was quite intimately associated with the destruction of a large amount of timber only partly defoliated by this caterpillar (133).

Later Evenden (32) recorded an infestation of western pine beetle following defoliation by this same pine butterfly (Neophasia menapia Feld.) near Spokane, Washington, in 1922-23. On the basis of a plot study, 26 percent of the defoliated trees died within 13 years after defoliation. More than half of the trees which died were attacked by D. brevicomis, the remainder dying from the effects of the defoliation alone.

The effects of defoliation by the Pandora moth on the Klamath Indian Reservation were studied by Patterson (100) following an epidemic in 1918-25. This moth defoliates the trees only on alternate years and does not destroy the terminal buds; as a result, most of the trees survive the effects of the defoliation alone. However, Patterson states:

> "The damage caused by bark beetle attacks in stands of pine defoliated by the Pandora moth has been far greater than the primary damage of the defoliator. Infestations of Dendroctonus brevicomis and D. monticolae have shown an abnormal increase in the defoliated areas studied. These infestations were of far greater intensity than were contemporary infestations in stands adjoining the defoliated areas, and beetle attacks upon defoliated trees were always fatal."

Scale Insects

The capacity of several species of the genus *Matsucoccus* to form lesions in the smaller twigs, resulting in a sudden killing of individual twigs and small limbs known as"flagging," has been recognized since 1934. This injury causes thinning and deterioration of the crown which suggests the possibility that it is a contributing factor to the attractiveness of pines to bark beetle attack.

The first species of this group to be studied intensively was *Matsucoccus vexillorum* Morrison in connection with a trouble prevalent in ponderosa pine through the southwest known as "twig blight." However the relation of the injury caused by this species to possible attraction to bark beetle infestations was soon found to be entirely negative.

Later McKenzie (U165) found that another species *M. bisetosus* Morrison produced lesions and resining in the axils of the twigs of ponderosa and Jeffrey pines which resulted in deterioration of the crown very similar to the characters recognized in "high risk" trees which are known to be susceptible to western pine beetle attack. McKenzie (81) pointed out that "this scale insect may be one of the important factors in the decadence of mature ponderosa pine and Jeffrey pine forests." This led to an investigation of the prevalence of scale infestations in high risk trees in the eastside ponderosa pine stands in northeastern California and the possible role of scales in causing high risk characteristics.

This study was undertaken in 1940 and was first reported upon by J.W. Johnson (U105). It consisted primarily of "a survey of the distribution of Matsucoccus populations in (a) the crowns of Risk I and Risk IV ponderosa pine trees, and (b) in unhealthy areas of crowns." This survey was supplemented by life history studies and by tests to determine the effect of injuries produced by the scale on the conductive properties of the twig stems.

A summarization of this study, up to the point where it was discontinued in 1942, was prepared by McKenzie (U166). The more significant points brought out in this report indicated that:

> "according to the data thus far accumulated as to the number of scales per square inch on the stems of low and high risk trees, there does not seem to be any particular significance in the Matsucoccus population in different parts of the crown. On the other hand if the extent of resining in the axils of the twigs from these trees is considered, the heavy axil resining does appear to be more prevalent on high risk trees than it does on those of low risk."

The scale study in general was inconclusive in establishing any relation between scale infestation and subsequent attack by the western pine beetle.

Needle infesting scales such as *Phenacaspis pinifoliae* (Fitch) and *Nuculaspis californica* (Coleman) have at times in restricted localities been found to cause defoliation and stunting of needle growth of ponderosa pines. Although no serious studies have been made and no reports are available, general observations of western forest entomologists tend toward the conclusion that these infestations have no bearing upon western pine beetle attack. One area near Susanville, California, is recorded in the Hopkins note system (Hopk. U.S. No. 17910) where an infestation of the above species stunted the growth of a stand of ponderosa poles during the period from 1922 to 1934. When these trees finally died, they were attacked by flatheads, and not by *D. brevicomis*.

Aphids

Aphids have been considered as a possible factor in bringing about the deterioration of pines and their susceptibility to bark beetle attack. However, no evidence has been produced to support this assumption. West (U311) made a study of a heavy aphid infestation on ponderosa pine near Prescott, Arizona. His report discusses the injury to the stems caused by the feeding of these sucking insects, but fails to establish any relation to susceptibility of the trees to bark beetle attack.

Resin Midge (Retinodiplosis sp.)

This insect causes the dying of twigs and the stunting and deformation of small branches so that the effect of the injury is to cause considerable deterioration of the crowns of heavily attacked trees. It has not been shown, however, that this induces attack by bark beetles. The resin midge has been found to restrict its attack to young trees and to the lower limbs of larger trees so that its injury probably does not have much effect on the vigor of the larger trees which are usually selected by pine beetles.

Composition Studies of Mixed Infestations

Common Infestation Types

The distribution of the attacks of associated cambium-feeding insects on the main bole of an infested tree is found in many varied patterns, depending on the bark area occupied by each species and the timing of the attacks. It has been found that when the infested bark surface is mapped according to distribution of insect species, a series of infested trees can usually be grouped into a few recognizable infestation types. These types may vary in their composition between areas and between seasons in the same area. However, there are a few standard patterns of attack that are usually found in any infested area. These more common infestation types are represented by diagrams in Figure 24, Type 1 in this figure, made up of pure D. brevicomis infestation without any associated insects, is usually found less frequently than types 2 to 5.

✓

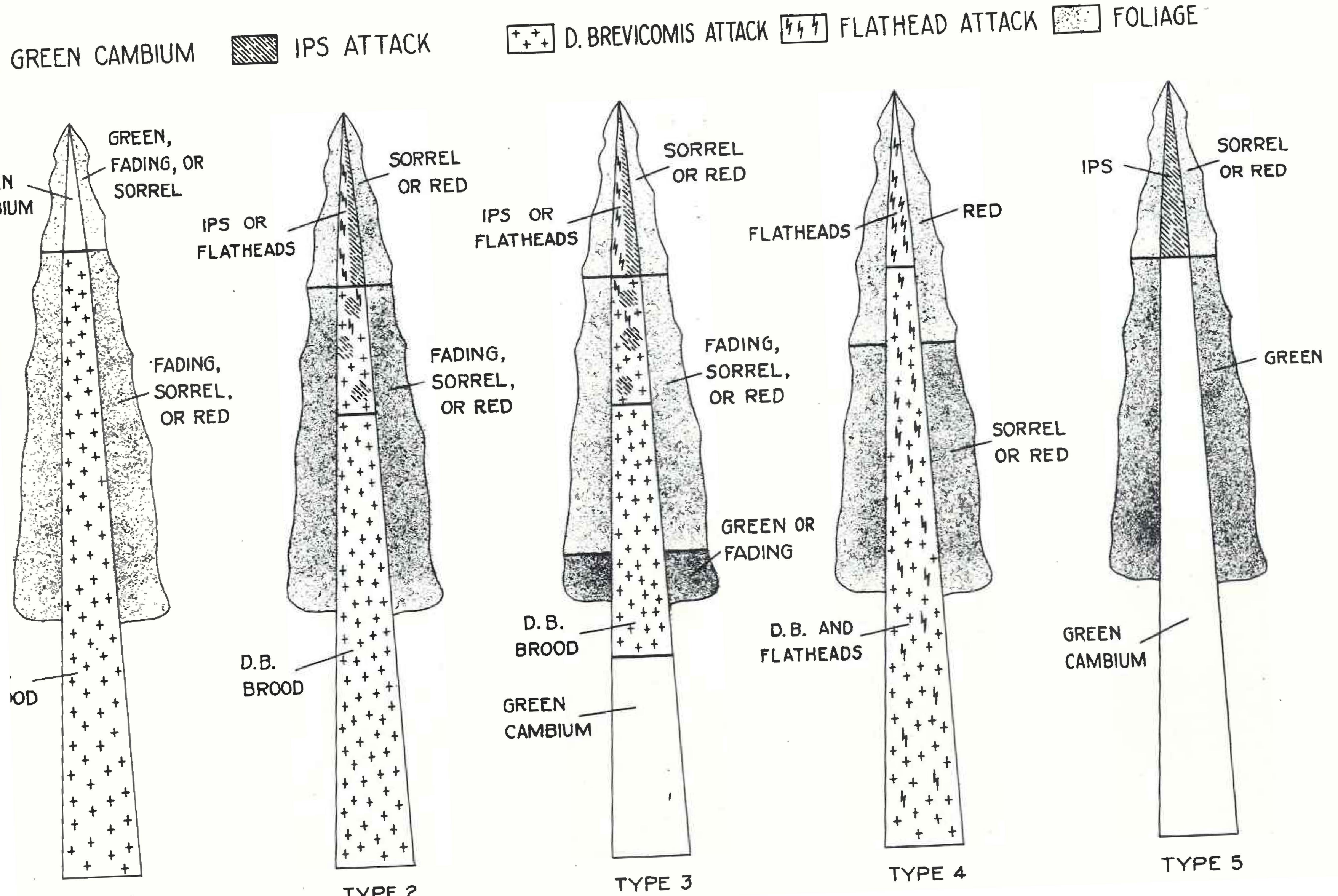
Figure 24 .—Infestation types - ponderosa pine.

Composition Types Found in the Earlier Studies, 1912-1918

This association of the western pine beetle with other insect species was first noted and studied in the first western pine beetle control projects on the Klamath National Forest in 1912. Burke (U43) in a summary of 514 treated tree records on the Craggy Mountain area shows that pure infestations of the western pine beetle were found in but 16 percent of the trees, of the mountain pine beetle in 2 percent, and of the flathead borer (Melanophila sp.) in 22 percent, making a total of 40 percent of the trees killed by one species of insect. However, mixed infestations of the western pine and mountain pine beetles were found in 3 percent of the infested trees; the flathead borer in 33 percent; a mixture of the western pine beetle, mountain pine beetle, and flathead borer in 10 percent; and a mixture of the mountain pine beetle and flathead borer in 14 percent. Altogether 60 percent of the total number of infested trees were attacked by various combinations of these mixed infestations. ✓

(Page 274a follows)

Figure 24.-- Infestation types - ponderosa pine.


GREEN CAMBIUM
▨ IPS ATTACK
D. BREVICOMIS ATTACK
FLATHEAD ATTACK
FOLIAGE
N
IUM
GREEN, FADING, OR SORREL
FADING, SORREL, OR RED
OD
SORREL OR RED
IPS OR FLATHEADS
FADING, SORREL, OR RED
D.B. BROOD
TYPE 2
SORREL OR RED
IPS OR FLATHEADS
FADING, SORREL, OR RED
GREEN OR FADING
D. B. BROOD
GREEN CAMBIUM
TYPE 3
FLATHEADS
RED
SORREL OR RED
D. B. AND FLATHEADS
TYPE 4
IPS
SORREL OR RED
GREEN
GREEN CAMBIUM
TYPE 5

Keen (U129) made a quantitative analysis of the infestation in the Ashland areas which had developed from a top-killing epidemic starting in 1914. He recognized the mixed character of most of this infestation and defined the various combinations of species which composed it from year to year. By sampling the infested bark area of a large number of trees, he worked out the relative quantity of each species involved. He allocated as "primary" the insect which he considered to be responsible for the final death of the tree. In his summary covering the seasons of 1914, 1915, and 1916, Keen states: "Ips attack preceded D. brevicomis attack in 96 percent of the total trees killed (578)." However, in this total number of trees killed, he found that "D. brevicomis was primary in 49.5 percent. Ips confusus was primary in 39.5 percent. D. monticolae was primary in 8.8 percent. Flathead borer was primary in 1.6 percent. Ips emarginatus was primary in .6 percent." In the trees considered to have been killed by D. brevicomis, Keen recognized combinations of attack by D. monticolae, D. valens, Ips confusus, Ips emarginatus, and flatheads as secondary species.

Mixed infestations in the southern Sierra westside region were studied on control projects carried out on the Sequoia National Park in 1918. Miller (U172) summarized the treated tree records from 87 ponderosa pines that were felled on the Kaweah Project in spring control work. He first grouped the trees according to the primary insect as recognized in the first examination by the spotters and compared this grouping with the infestation that was found by examination of bark on entire length of the bole after the trees were felled. This comparison is shown by the following table:

Basal examination	No. of trees	Infestation found after trees were felled	No. of trees
D. brevicomis primary	71	*D. brevicomis* only	43
D. monticolae primary	6	*D. monticolae* only	6
Unknown (base green)	10	*Ips confusus* and *Ips oregonis*	4
		D.b. associated with *D.m.* and *Ips* in tops	28
		Topkills ⊖ trees would have survived if not felled (*Ips*)	6
	87		87

This comparison brought out the point that for this area and type of infestation, the basal examination by no means gave a reliable index to the species of insects that attack the main bole of the tree.

The Devil's Garden Study, 1928-1934

In 1928 a small isolated area of ponderosa pine type in the Modoc National Forest was selected for an intensive control experiment. The original purpose of this project was to determine the possibility of completely eradicating *D. brevicomis* in an area that was isolated on all sides from other infested areas by a continuous break in pine type. The project became known as the Devil's Garden Extermination Experiment. The results have been reported by Keen (U139,U141), Salman (U250,U259), and Johnson (U115,U116,U117). Control work was initiated in the spring of 1929 and during the seasons of 1929 and 1930 all of the infested summer and winter brood trees that could be found were treated by the cut-peel-burn method. Thereafter the overwintering brood trees were thoroughly treated each spring up to and including the 1931 overwintering generation.

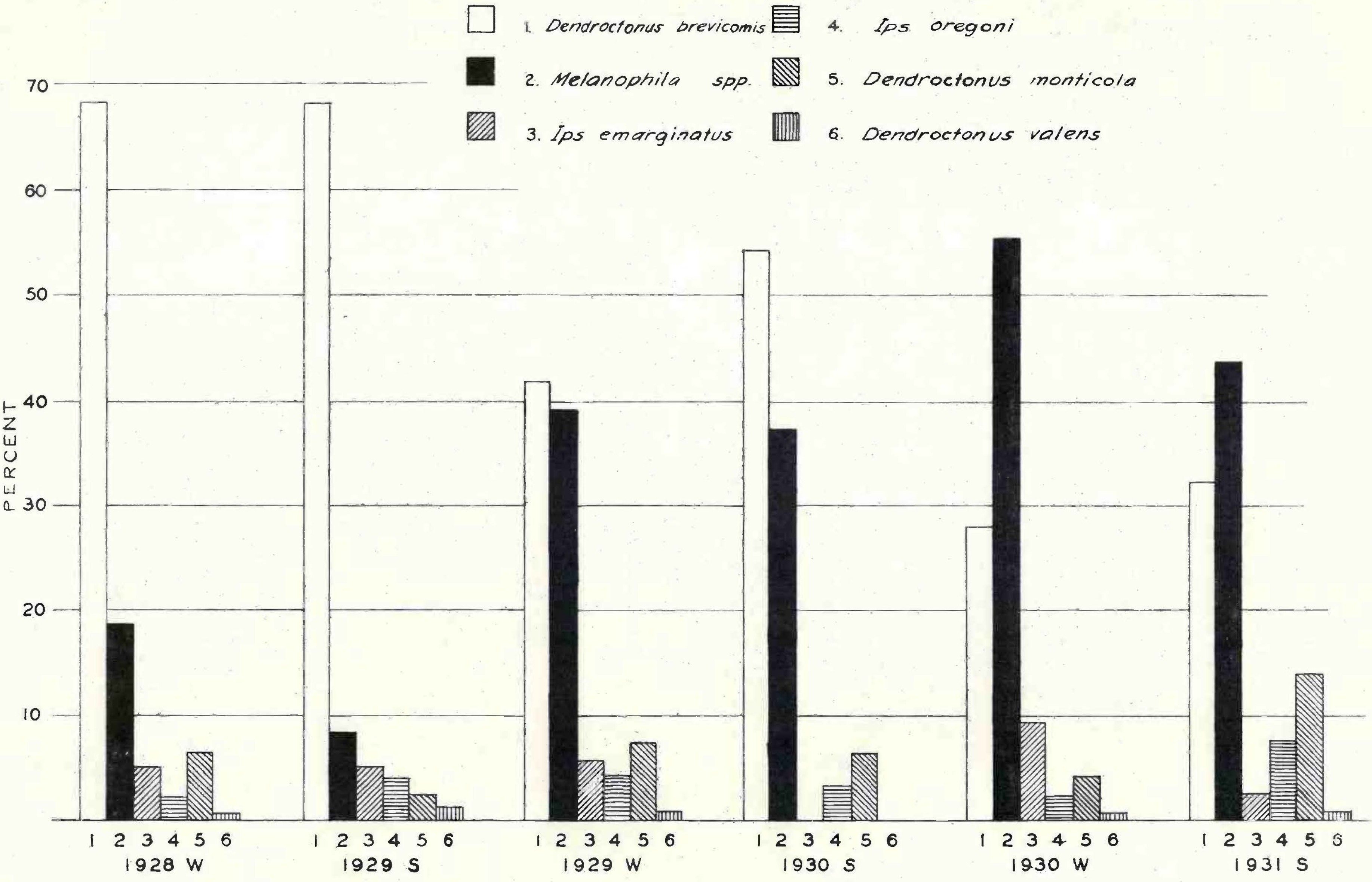
One phase of the project was a study of the composition of the infestations which developed in the area during and following control work. Records were maintained of the amount of bark surface infested by six species of associated insects including *D. brevicomis*, *D. monticolae*, *D. valens*, *Ips emarginatus*, *Ips oregoni*, and *Melanophila* spp. It soon became apparent as the project progressed that the relationships of these species were not static but changed from year to year.

The importance of the species associated with *D. brevicomis* is illustrated in Figure 25, which shows the percent of total bark surface infested by each species during each successive generation, beginning with the overwintering generation trees of 1928 and ending with the summer generation of 1931. This graph shows a change in the relative volumes of the six species with each succeeding generation. The most significant point developed by the study was that as *D. brevicomis* was reduced in the area by intensive control work, the pine flathead increased in importance and eventually became the dominating species. In the overwintering brood trees of 1931 (not shown in figure 25), the flathead population occupied 69 percent of the infested bark surface and *D. brevicomis* but 11.1 percent. The two species of *Ips* and *D. monticolae*, however, did not show any significant trends during the period of the study.

Figure 25.--Percent of bark area infested - by Species

(Page 278a follows)

Figure 25- PERCENT OF BARK AREA INFESTED — BY SPECIES



Infestation Types in the Southern Sierra Sub-Region, 1930-1932

On the Sugar Pine Sale bark beetle project on the Sierra National Forest in 1931, the mixture of insect species comprising the attack became an important consideration in determining control policy. This project was undertaken to control a widespread epidemic of the western pine beetle in the southern Sierra region which started in 1930. Heavy topkilling by *Ips* preceded the main attack of the western pine beetle on the control area. In the execution of the control measures, it was necessary to decide whether or not the trees infested only by *Ips* in the tops or by *Ips* in combination with a very light infestation of *D. brevicomis* should be treated. Apparently such top-killed trees stood a good chance of survival unless attacked in the main bole by *D. brevicomis*. In his report on this operation, Gustafson (U73) discussed the composition of the infestation and its implications. The types that were recognized in the 1931-32 overwintering infestation during the period of the control work were illustrated by diagrams of representative trees, showing the bark areas attacked by the different species of insects. These types of infestation were listed in the order of their importance as follows:

1. *Western pine beetle - Ips confusus*.-- Top was attacked by *Ips*, western pine beetle mixed with *Ips* in the mid-bole and pure western pine beetle in the lower bole. *Ips* had apparently initiated the first attacks in the top; often the base was green and unattacked for 10 to 20 feet up from the stump. Trees of this type made up the great bulk of the overwintering infestation.

2. *Western pine beetle - flathead - Ips*.— Attacked by *Ips* in the top, a mixture of all three species in the mid-bole, and western pine beetle in the lower bole.

3. *Western pine beetle - flathead*.— Attacked by flatheads in the top, a mixture of western pine beetle and flathead in the mid-bole, and western pine beetle in the lower bole.

4. *Ips confusus*.— About 25 to 45 feet of top attacked by *Ips*, the entire lower bole green, and unattacked. These trees were primarily topkills with a good chance of survival, if not attacked later by the western pine beetle.

5. *Western pine beetle*.— Pure infestation of this beetle occupied the main bole. The top, from the six-inch diameter on up, was usually green and unattacked.

6. *Flathead* (*Melanophila californica*).— The entire bole was attacked by this species. This type was confined almost entirely to Jeffrey pine.

The general practice adopted on the control operation was to leave top-killed trees untreated (type 4) if less than 50 percent of the upper bole had been attacked. Studies made on this area two years later found that about 50 percent of the trees of this type had been attacked and killed by the western pine beetle since the control operation, but the remainder still survived as stag-tops.

The composition of this infestation in the Sierra areas changed very materially during the 1932 season according to Furniss (U62). Early in the spring following the control work, the Ips infestation was reduced to a minor role and by fall had almost completely disappeared from the area. The flathead infestation, however, maintained its ratio in the composition with D. brevicomis and became relatively more important.

Regional Studies of Composition, 1931-1935

Other records of composition were accumulated during a series of control projects during the period from 1931 to 1935. These studies still further emphasized the point that there is a wide difference in the abundance and behavior of the insect species making up the composition of the different types of infestation; and that these differences are related to region and to the phases of the epidemic cycle. The abundance of associated insects that initiate the first attacks during the earlier stages of an epidemic was considered by some observers to raise considerable doubt as to the importance of the western pine beetle as a primary species.

Because of the apparent significance of associated insects as a clue to the behavior of western pine beetle epidemics, records from various control projects and surveys throughout the California region were summarized and reported by Salman (U263). This summary included records from 782 infested trees on 11 different areas extending from northeastern California to the southern Sierra region. The character and amount of infestation by different insect species were determined by the sampling of some 361,160 square feet of bark on these trees.

Salman listed the following as the more important insects found in association with the western pine beetle throughout the region: D. valens, D. monticolae, Ips emarginatus, Ips oregoni, Ips confusus, Melanophila californica, and Melanophila gentilis. However, he found that pure infestations of the western pine beetle "infested over 40 percent of the bark surface of trees included in the samples. It entered into infestation of 67 percent of the entire bark surface. It is nearly 3 times as abundant as any other species." He also found that these pure infestations of the western pine beetle were common in eastside areas, but uncommon in westside areas. However, the beetle's habit of extending the attack to about the four-inch top diameter was common in both regions.

Figure 26 and Figure 27 illustrate a comparison of the infestation types between westside and eastside pine areas during the season of 1934. Control records were used to map the infested bark areas by insect species for all trees containing 1933-34 overwintering broods on Regional Survey Plot 7 (Cascadel area), representing the westside pine type; and the Badger Control Area (Modoc), representing the eastside type. These figures were drawn to scale based on the average diameter and height of trees making up each infestation type, so that the relative size of trees involved in the different compositions is shown. The percent of total infested volume which each infestation type composed is also illustrated in the figures.

Figure 26 .--Infestation types - ponderosa pine. Regional Survey Plot Seven, Sierra National Forest, California. Overwintering 1933-34 brood trees.

Figure 27 .--Infestation types - ponderosa pine. Badger Control Area, Modoc National Forest, California. Overwintering 1933-34 brood trees.

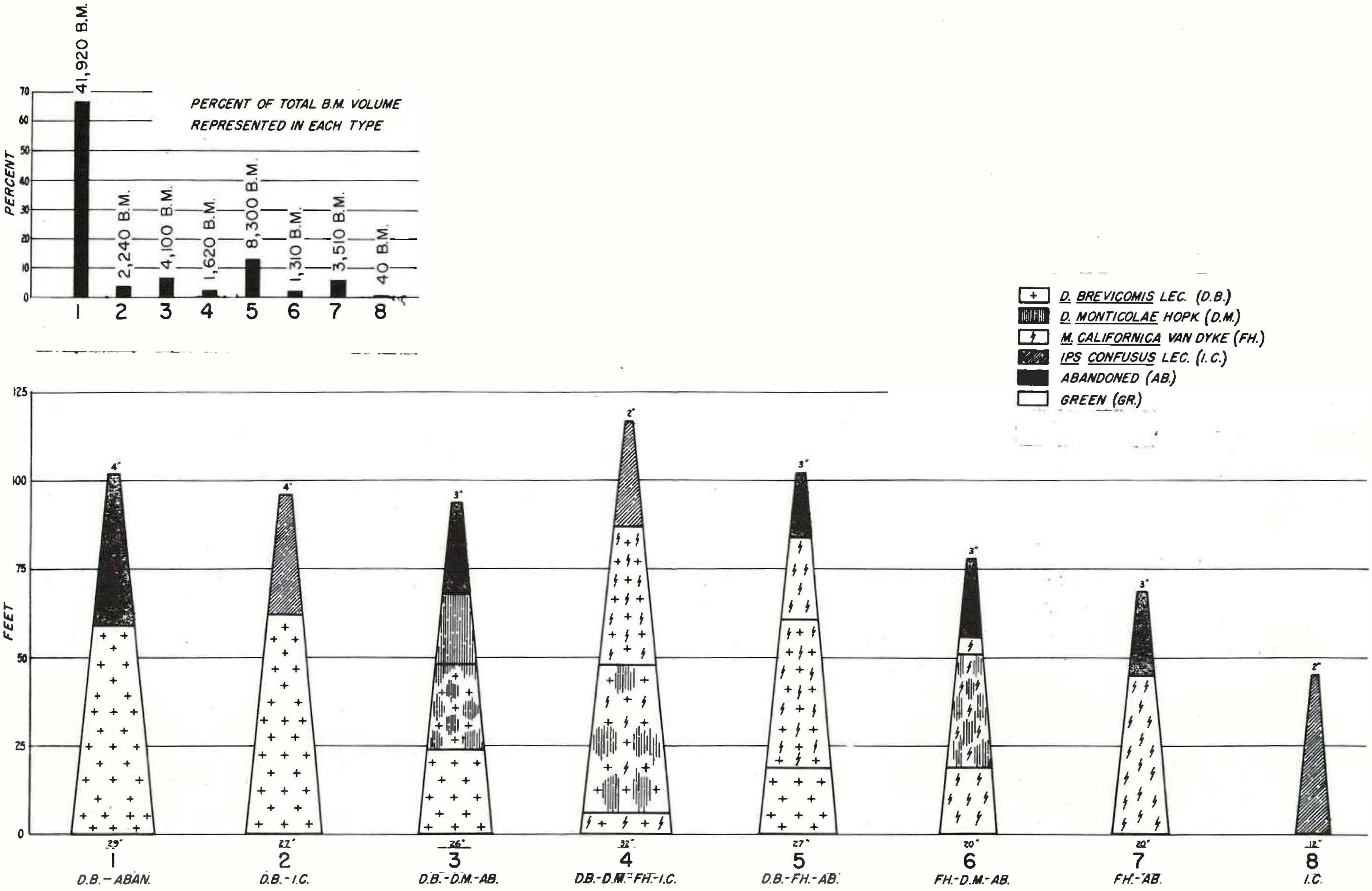
It was found that the westside infestation types were made up primarily of trees which had been initially top-killed, and at the time of the D. brevicomis attack were either infested or abandoned in the top by Ips and flatheads. In the eastside types, top-killing was a minor factor and the figure shows that four out of the eight types had no insect attack at all in the top. The eastside types were primarily a D. brevicomis-flathead composition with D. monticolae playing a more prominent role in the mid-bole than on the westside areas.

Salman recognized 22 combinations or types of mixed infestations of the above species, but listed the three following as the most important for the region as a whole.

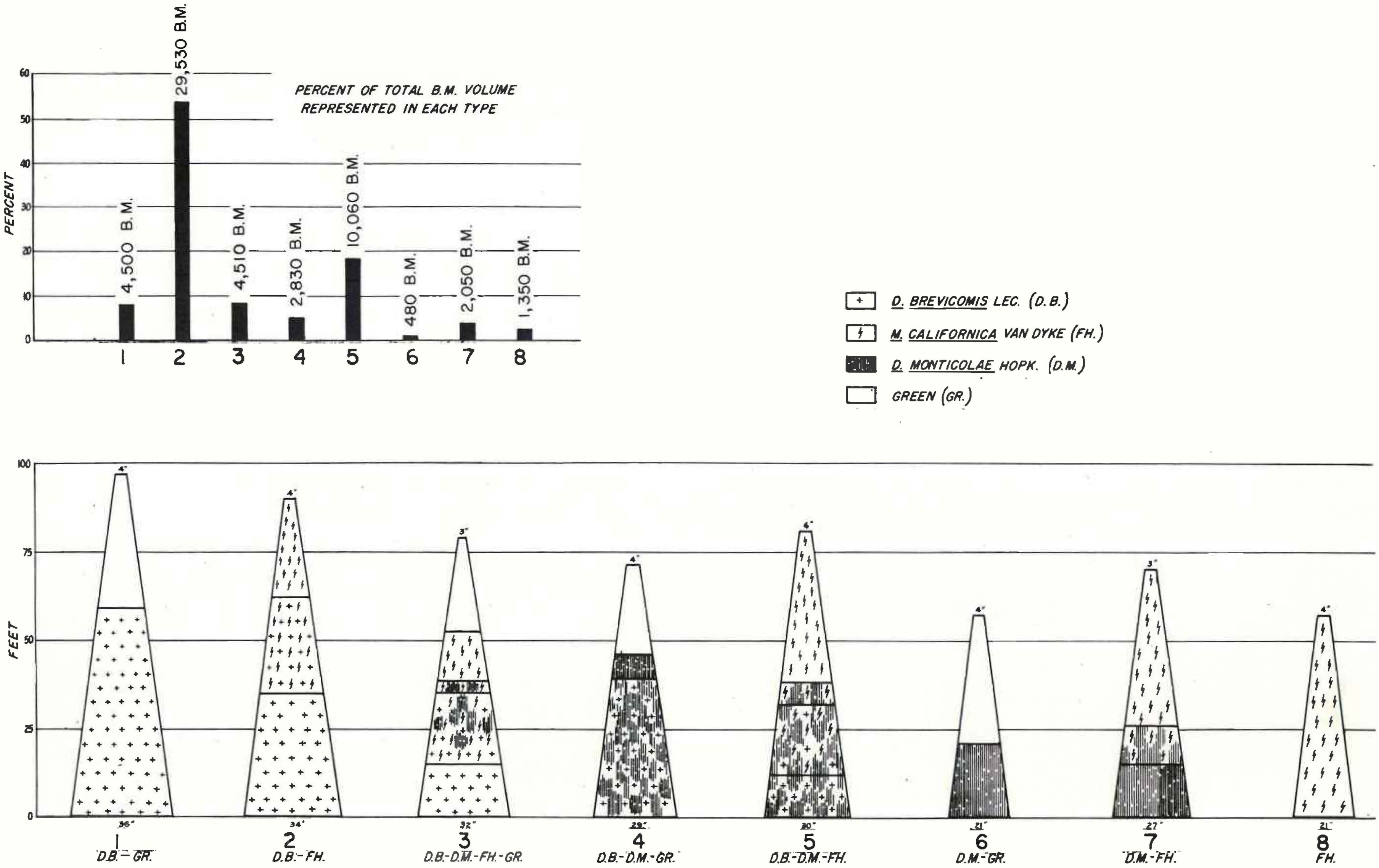
1. Western pine beetle - flathead borers.-- "This type of infestation was found to be the most important in eastside areas and fourth in importance in the westside areas. The combination of the 2 species may extend from the base to the top of a tree, or may exist with pure flathead infestation in the top, or pure western pine beetle infestation in the bottom. It also may exist only in the middle bole with pure flathead in the top and pure western pine beetle in the bottom."

(Pages 283a,283b follow)

Figur [illegible].-- Infestation types - ponderosa pine. Regional Survey plot seven, Sierra Natio[illegible] Forest, California. Overwintering 1933-34 brood trees.



Figur .-- Infestation types - ponderosa pine. Badger control area, Modoc National For
California. Overwintering 1933-34 brood trees.



2. Western pine beetle - engraver beetles.--

> "This combination was the more important in westside areas due to the outbreak of engraver beetles (Ips confusus) that occurred in those areas during the period of record. It is believed that the western pine beetle is secondary in these trees as many of them were of small size and the engraver beetle initiated the attack. In the eastside areas Ips oregoni is the species concerned. Evidence was found that the engraver beetles here followed the initial attack of the western pine beetle."

3. Western pine beetle - mountain pine beetle - flathead borers.-- "This mixture of species in which either the first or last named may be primary and the mountain pine beetle usually of secondary importance appears to be predominantly an eastside infestation type."

Salman pointed out that "marked differences in infestation composition are noted between the eastside areas, which lie in the 0-20 precipitation belts, and the westside areas that lie in the 20-40 inch precipitation belts." Infestation types of the eastside differ from those of the westside by "(1) the greater amount and importance of mixed infestations, (2) an increased importance of flathead borers, (3) decreased importance of engraver beetles, exclusive of Ips emarginatus, and (4) the western pine beetle entering into a greater proportion of the infested bark." He attributed these differences largely to variations in moisture supply.

The reliability of basal examinations as an index to primary insects attacking the main bole was another phase of this study by Salman. From the data covered he found that "basal examinations would determine the cause of death in the predominant infestation types in but 36 out of every 100 trees. Cruise results interpreted strictly on the evidence from basal examinations may show the relative abundance of a given species but not necessarily its importance." Salman recognized that "the western pine beetle is the most abundant insect concerned in forest insect infestations of ponderosa pine in California," but thought that "its primary importance may be overrated... The data show that so-called secondary species, particularly Ips confusus and Melanophila californica may, in infestations over relatively large areas be the primary species and cause the death of the majority of infested trees."

The infestation studies were not carried on over a long enough period of years to show the significance of variations in composition from year to year, or to obtain clues as to what such variations might mean as indicators of changes in the infestation cycle.

Studies of Infestation Types in Eastside Areas of Northeastern California, 1937-1941

From these preliminary studies it was recognized that the changes from year to year in the relationships of insects associated in the attacks upon ponderosa pine might be of significance in infestation cycles and for this reason composition studies were continued after 1935 in northeastern California. These studies were given considerable impetus by a growing realization of the importance of the flathead, Melanophila californica in the ecology of eastside pine stands.

The basis for the data was a selected sample area which was covered each year and on which the infested trees were felled and areas of infested bark measured. As stated by J.W. Johnson (U119),

> "The studies of species relations in the infestations of ponderosa and Jeffrey pines were begun because of a need for more knowledge of such phenomena than had been obtained from the usual field examinations of standing trees. Attention was directed to 4 specific objectives.
>
> "1. To determine what insect species had attacked the trees.
>
> "2. To determine the sequence of the attacks of different species on trees and their interrelationships in the infestations.
>
> "3. To determine the relative frequency of the different species, and the fluctuations in their numbers from year to year.
>
> "4. To discover the infestation patterns characteristic of the different years."

In 1938 West (U316) reported upon composition studies made during the 1937 and 1938 seasons on the Modoc National Forest. He noted a difference in the grouping tendency of attacks between these two seasons. In 1937, 12 percent of the attack trees occurred in groups while 44 percent of the 1938 trees were grouped. The principal species involved in these infestations were *D. brevicomis*, *D. monticolae*, *D. valens*, *Ips oregoni*, and *M. californica*. Of the trees selected for attack in 1937, 37 percent had been previously topkilled, as against 42 percent in 1938. *Ips oregoni* was found to be important as a fill-in species in trees initially attacked by *D. brevicomis*. *M. californica* was found in 61 percent of the trees attacked in 1937, but in 1938 it occurred in only 41 percent.

In 1940 J.W. Johnson (U106) compared the trends and composition of infestations that developed during the 1939 and 1940 seasons on the same sample area on the Modoc. These two seasons were characterized by fairly low infestations and by a marked decline in the volume of trees killed in 1940 from that of 1939. This decline was accompanied by recognizable changes in the composition of the attack. This is best illustrated by the following table in which the species initiating the attack is listed first with each infestation type.

Infestation type	Percent of total trees	
	1939	1940
M. californica - *D. brevicomis*	14.1	39.5
M. californica - *D. brevicomis* - *Ips oregoni*	14.2	25.6
M. californica - *D. monticolae* - *D. brevicomis* - Misc.	8.4	2.3
D. brevicomis only	18.3	9.3
D. brevicomis - *Ips oregoni*	45.1	14.0
Ips oregoni - *D. brevicomis*	2.8	7.0
D. monticolae - *D. brevicomis*	5.6	-

Johnson compared the composition that occurred during the two seasons in trees attacked in groups with those attacked singly, and found that:

> "D. brevicomis had a higher incidence in group trees than in single trees, and its incidence in both classes of trees decreased from 1939 to 1940. *Melanophila californica* had a higher incidence in single trees than in group trees, and its incidence shows an increase from 1939 to 1940. *Ips oregoni* shows its highest incidence in group trees and shows a slight increase from 1939 to 1940. But it is noteworthy that the *Ips oregoni*'s general occurrence in all infestations, both as an initiating species and as a supplemental species, was less (46.5 percent) in 1940 than in 1939 (53.5 percent). *D. monticolae* disappears from the picture in 1940. In 1939 its incidence was slightly higher in single trees than in group trees."

In 1941 Johnson (*U110*) made a composition study of infestation types in both ponderosa and Jeffrey pines on the Lassen National Forest covering the two seasons of 1940 and 1941. Points brought out in his summary for this area included the following:

> "Dendroctonus brevicomis was the most frequent species in the infestations in both years.
>
> "Melanophila californiea was the second most frequent species in both years.
>
> "Dendroctonus monticolae, Ips emarginatus, Dendroctonus valens and Ips oregoni were of common occurrence in the infestations; the first three species being relatively more numerous in 1941 than in 1940.
>
> "Jeffrey pine was infested with Dendroctonus jeffreyi for the most part, although Melanophila californica appeared to have initiated attacks in 4 trees. Ips emarginatus, Ips oregoni and D. valens were present in the infestations also."

Summary of the Composition Studies

J.W. Johnson's studies were the last of the composition surveys and in attempting to appraise the value of the work he stated: "From the composition studies has come a better appreciation of the complexity of the inter-insect and inter-tree relationships that develop during the death of the tree from insect attack."

So far as the studies have developed, the understanding of species relationships in mixed infestations has not been carried far enough to warrant its use in appraising the status of current infestations and in forecasting trends. However, the following conclusions appear to be warranted from the data that have been collected.

1. Practically all of the D. brevicomis infestations that have been studied are of the mixed type with the associated insects playing a prominent role.

2. Basal examinations have served as a reliable index to the type of infestations in the main bole of the tree in less than half of the cases (only 36 out of every 100 trees). In bark beetle surveys, the judgment of the spotter must largely determine the type of infestation in the trees that are marked as infested.

3. Where infested lengths have been studied, great variation has been found in composition of the infestation from season to season and between areas.

4. There is good evidence that the relation of species composing a current infestation may serve as an index to coming trends. When the season is marked by aggressive top-killing by Ips or flatheads, an increase of D. brevicomis will follow (as on the Sierra area); when D. brevicomis occupies nearly all of the infested bark surface and Ips and flatheads are a minor factor, a decline of losses may follow (as on the Modoc). However, composition records have not been continued long enough over consecutive seasons in the same areas to establish their reliability in the prediction of trends.

5. Enough data have been collected to show that D. brevicomis is the dominating species in the composition when the peak of an epidemic is reached.

6. The work of obtaining accurate bark surface measurements to show the composition of a mixed infestation on a quantitative basis is time consuming and obviously impractical in survey practice. This factor has obviously discouraged the use of composition analyses as a basis for determining the expected trend of infestations.

EPIDEMIOLOGY OF THE WESTERN PINE BEETLE

The Interaction of Biotic Factors

It has already been shown that the biotic factors that act directly on the beetle by limiting or favoring its abundance include temperature, parasites and predators, diseases, competitors, associated insects, weather conditions during flight, and the inherent tropisms and habits of the beetle; these all go to make up a very complex group of influences. Seldom can any one factor be singled out as dominant in any given situation; many of them are compensating and their net effect is nil. In addition to these biological factors, environmental or ecological conditions are known to have indirect, but important, effects upon beetle populations. These will be discussed later.

The interaction of all these forces, favorable and unfavorable, to the beetle, is reflected in the changes of population density which in turn are reflected in the amount of timber killed in any given area each year. Salman and Bongberg (U267) undertook to analyze changes in population density in the light of what had been learned about the biology of the beetle and stated:

> "The fluctuations in timber loss supposedly caused by the western pine beetle go to make up what are known as infestation cycles. The increases, as they have occurred, have largely been considered due to the potential power of the insect species or to the susceptibility of the host trees. The decreases in the loss record have largely been considered due to the reduction in populations of the western pine beetle, a resistance of the host trees, or adverse climatic factors. At times sudden changes are inexplainable. Three years of study of the biology of the western pine beetle has indicated that the story of the fluctuations that occur in the records of insect-killed ponderosa pine is not a simple one."

Periodicity Studies

Even though the causes cannot be determined, a knowledge of the frequency with which epidemics or high peaks of population occur is of advantage in dealing with the western pine beetle problem. To know when to expect outbreaks would give the owner of threatened timber an opportunity to prepare for control work or for utilization of stumpage before it is killed. This possibility of forecasting changes that are to come has been one incentive for the maintenance of long-term survey records in which the rise and fall of beetle populations have been measured by the amount of timber killed annually.

Rogue River Studies, 1914-1924

The first study of western pine beetle epidemiology was started at Ashland, Oregon, in 1914. Dr. A.D. Hopkins, then in charge of the Division, designated the study as "Project 15a." The first preliminary studies were started by Keen (U129), who made a quantitative analysis of the infestation on the Lamb's Mine Unit of 3,200 acres for the seasons of 1914, 1915, and 1916. Keen itemized the types of infestation involved in the timber losses on this unit and the changes in quantity from season to season. Losses were rising during most of this perod and Keen pointed out that "this quantitative study will become more valuable when the quantity for the next few years is measured each year."

The Lamb's Mine area, however, was suspected of being too small a unit for an adequate sample of the broad infestation trends in the pine type. The study was therefore expanded in 1916 to cover approximately 350,000 acres, more than half of which was ponderosa pine type, in the Rogue River, Applegate River, and Klamath River watersheds. This general area, which was grouped around the Ashland Station, contained a wide variety of climatic and site conditions and was considered large enough to represent any significant changes in trends that might occur during the life of the study.

The first report for this enlarged area was prepared by Miller (U170), who stated that one purpose of the study was to determine "the character, periods of time involved in, and the causes of the intermittent increase and decrease in the annual amount of infestation."

The Rogue River and Klamath areas were divided into a series of 19 watershed units in each of which the timber losses were measured separately; the Applegate area, in which the pine type was much scattered and broken, was treated as a whole. The loss records on all of the areas covered began with the 1914 season, although on two of the Klamath units old loss cruises carried the record back to 1911. The intensity of survey coverage varied in the different areas. Most of the Rogue River units were cruised intensively; the Applegate watershed was covered by extensive reconnaissance; and in the Klamath area two units were covered by intensive loss surveys, while the remainder were covered by extensive methods. In all areas the basis upon which the final estimates of losses were arrived at were considered to be of sufficient accuracy to reflect trends.

A second report was prepared by Miller (U175) in which he summarized the results established by four years of records, 1914-1917, inclusive, as follows:

> "Dendroctonus brevicomis is by far the most important enemy of the pine and is responsible for 90 percent of the total annual loss. The loss caused by this insect does not remain constant, but is subject to great fluctuations from year to year. In this study the D. brevicomis infestation underwent a distinct cycle or epidemic covering a period of 4 years, during which a pronounced increase was followed by a corresponding decrease.
>
> "The epidemic which has been studied ran through approximately the same cycle throughout the entire project area of 350,000 acres. The cycle of the infestation within each of the small tributary watersheds which have been termed units was nearly uniform throughout the project area. The high-water mark of the epidemic occurred in 1915 on some units and in 1916 on others. But we do not find a single case of any unit declining to a low point in 1915 or 1916, but in all units studied the epidemic started upward in 1914 and declined in 1917. This indicates that the factors which influence the rise and decline of epidemics are not confined to small local centers or watersheds, but operate throughout great forest areas."

The results of this four-year study indicated rather definitely that it was unnecessary to cover so large an area to obtain a record of trends within a region. The recommendation was made, therefore, that the Applegate and Klamath areas be dropped from the surveys, but that the study on the Rogue River area be continued "until such time as sufficient data on all phases of the infestations were secured to make possible the forecasting of epidemics and their probable duration." These studies were continued by Patterson (U212) until the close of the 1924 season. Patterson's 1924 report summarized the infestation cycles that had occurred in the Rogue River area during the 11-year period from 1914-1924, inclusive.

> "The first epidemic infestation occurred in the years 1915 and 1916, killing during this period 1.9 percent of the stand. This was followed by a decline of 56 percent during 1917. In 1918 the infestation again became epidemic, killing .7 percent of the stand; an increase over 1917 of 78 percent. From 1918 the infestation gradually declined with minor fluctuations until 1923, when it reached the lowest point recorded, killing only .13 percent of the stand. From this point the infestation showed a decided upward trend and in 1924 made an increase over 1923 of 82 percent. The infestation may continue to mount in 1925 or it may decline as it did following the 78 percent increase in 1918.
>
> "One striking feature of the progress of the infestation is the regularity of the 4-year cycles. Beginning with the low point in 1914, the subsequent low points in 1917 and 1921 showed 3-year intervals. Likewise the peaks occurred every fourth year beginning with 1915 and followed by the peaks in 1918 and 1922. If the study of other infestations show similar results, we may expect relatively high infestations with heavy losses every fourth or fifth year."

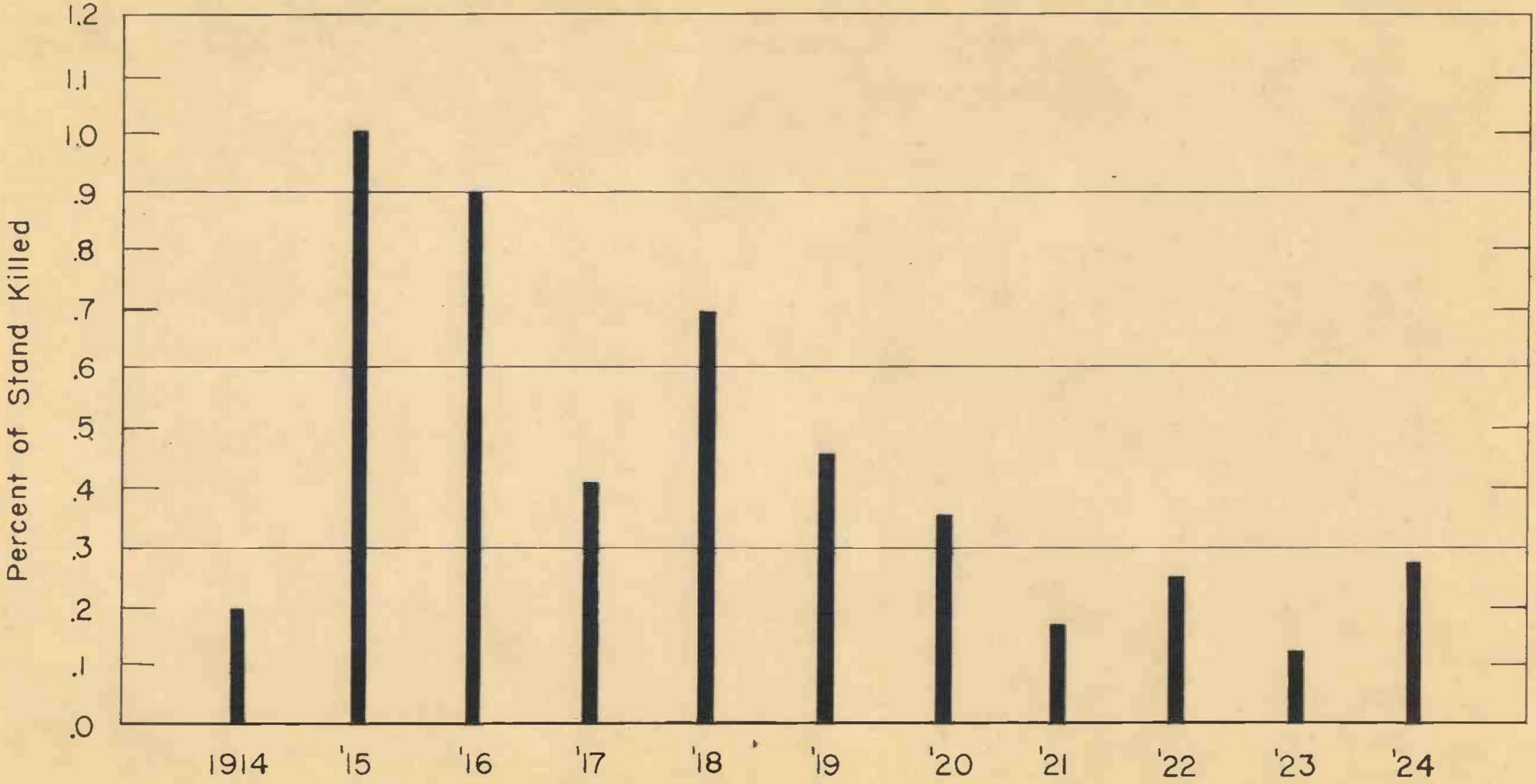
The percent of stand killed annually on the entire area and the loss cycles mentioned by Patterson during the period 1914-1924 are shown in Figure 28.

Figure 28.—Western pine beetle infestation trend on Rogue River area, Oregon, 1914-1924.

The Rogue River study was discontinued in 1925, both because of the pressure of control surveys in other areas and because the mature pine type of many of the Rogue River watersheds had deteriorated, as a result of wood cutting, timber operations, and beetle losses, to the point where it was no longer suitable for a study of undisturbed infestation trends.

(Page 296a follows)

Figu 8.--Western pine beetle infestation trend on Rogue River Area, Oregon. 1914-1924.



The Klamath Basin Records, 1921-1952

The Klamath Basin surveys were inaugurated as early as 1911, but for the first 10 years data were of an observational nature and did not provide the quantitative basis for an accurate interpretation of infestation trends.

In connection with the Southern Oregon - Northern California Pine Beetle Control Project, check plots were established in 1921, scattered over the main ponderosa pine forests of Klamath and Lake counties, Oregon. While the control project was underway, 120 section plots were cruised to determine the general trend of the infestation and the need for control in different units. A territory of about one million and a quarter acres was involved which was divided into three areas approximately equal in extent. On some plots the loss record was extended back to 1918 on the basis of control surveys.

After the cooperative control funds were exhausted and each agency continued control work independently, such a large cruising program could not be continued and various sections were dropped. Year by year, with the advance of logging operations, other plots had to be dropped until by 1933 only 25¼ sections remained to continue the record of annual losses. The statistical record of losses on the plots and the estimates of total annual kill from 1921 to the close of the 1932 season were covered ina series of reports by Keen (U135, U146). Subsequent annual surveys have continued the loss record in this region up to the present time.

In his report for the 1931-32 seasons, Keen (U146) reviewed the 11-year loss record from 1921 to 1931 and made a preliminary analysis of the more evident trends:

> "As has been pointed out several times before, the trend of bark beetle infestation has not been uniform over the entire area represented by the sample plots, even though the growth pattern has been practically identical for the entire area.
>
> "Thus area 1 plots reached a high point in 1925, decreased to a low in 1928, increased slightly in 1929, dropped again in 1930, and started up again in 1931.
>
> "Area 2 plots reached a high point in 1926, decreased steadily to a low in 1930, and then started up in 1931.
>
> "Area 3 plots reached a high in 1927, dropped suddenly to a low in 1929, and then started up in 1930.
>
> "Evidently there is a complicity of factors which determines epidemic trends; and while tree resistance is an important one, the character of the stand, the amount of recent bark beetle losses, and the action of predators all have their influence in determining the course of a beetle epidemic.
>
> "Moreover, climatic factors are of prime importance as is so well illustrated by the effect of the recent low winter temperatures which destroyed a high percent of the bark beetle broods throughout the pine region of eastern Oregon."

Following 1931 the infestation in the Klamath Basin continued to increase and reached a new high in 1932; then dropped in 1933 due to a freeze in the winter of 1932-33; recovered somewhat in 1934; then continued to drop to a new low in 1937. After 1937 the infestation increased to a minor high in 1939 and then dropped to an all time low in 1942. This was the lowest point reached since records were started in 1921. Since 1942 the infestation has continued at an endemic level for 10 years, never exceeding an annual loss of more than 0.60 percent of the stand per year. The infestation trend for 30 years in the Klamath Basin is shown in Figure 29.

Figure 29 .--Trend of western pine beetle infestation in the Klamath Basin, Oregon, 1921 to 1952.

About 1930, it was thought that the infestation trends in the Klamath Basin gave support to the theory of a six-year cycle with lows in 1917, 1923, and 1929. But subsequently lows occurred in 1933, 1937, and 1942, which were four, four, and five years apart, and since 1942 a state of low endemic infestation has been continuously maintained for 10 years. Thus the theory of epidemic cycles breaks down and we must look elsewhere for explanations of the rise and fall of epidemics.

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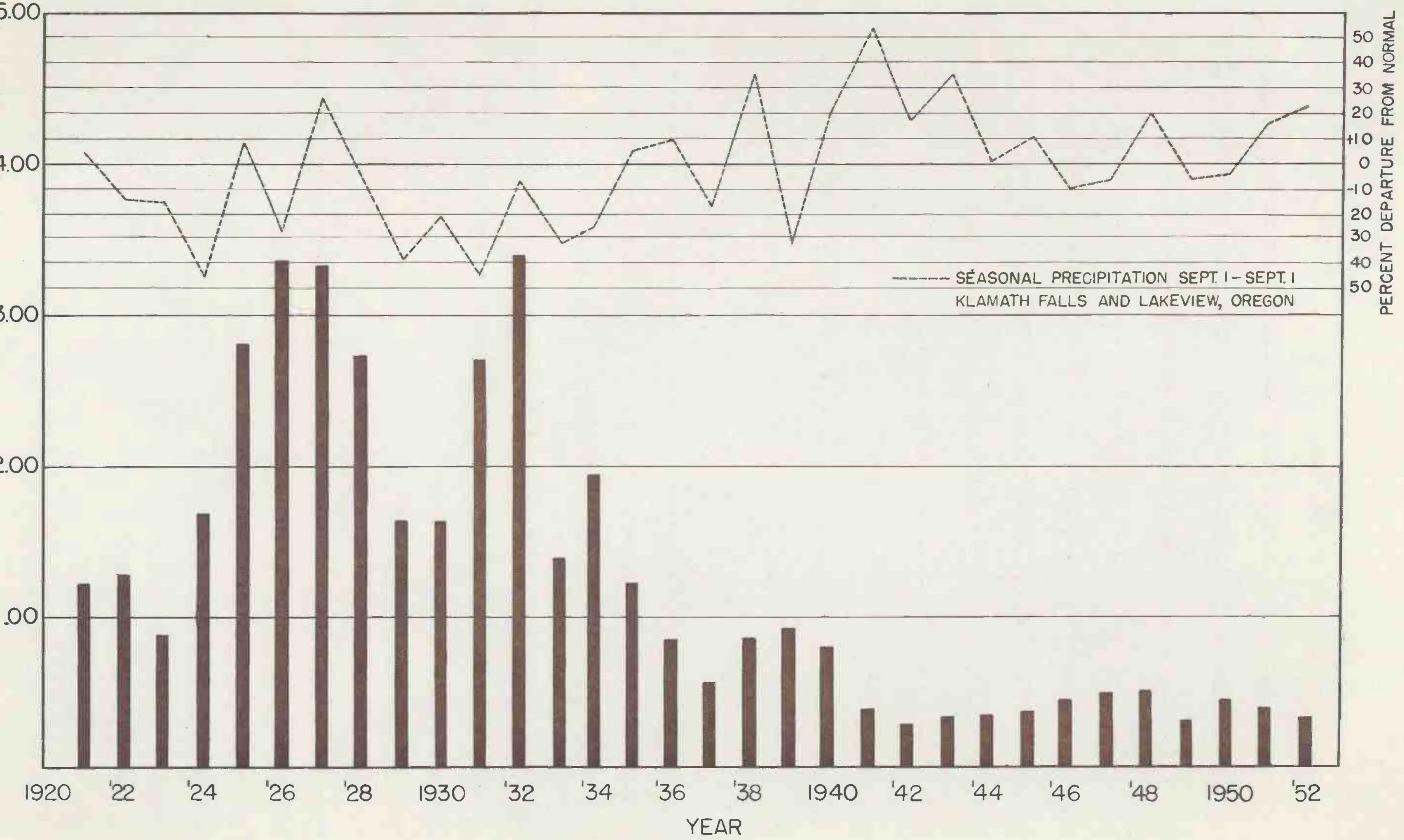


Figure 29.-- Trend of western pine beetle infestation in the Klamath Basin, Oregon, 1921 to 1952.

Northeastern California Records, 1921-1943

A similar continuing record of measured and estimated losses began on the Happy Camp-Lava Beds area of the Modoc and Shasta National Forests in 1921. Similar surveys were started on the Eastern Lassen and East Plumas National Forest in 1929. Although many of the original plots have been lost through logging operations, annual surveys have been maintained which provide an estimate of the board foot loss per acre on virgin stands for each season up to the present time.

The board foot per acre loss of ponderosa pine due to western pine beetle infestations on the Happy Camp-Lava Beds area of the Modoc National Forest, California, for the period 1921 to 1949 inclusive is shown in Figure 30 . Peak losses occurred in 1927 and 1934. There is a striking similarity in the trend on this area and the neighboring Klamath Basin, Oregon, area shown in Figure 29 . The trend of loss on four individual units of the Happy Camp-Lava Beds area is shown in Figure 31 for the period 1921-1935.

Figure 30 .—Trend of western pine beetle infestation on virgin ponderosa pine sample plots, Happy Camp-Lava Beds area, Modoc National Forest, California, 1921-1949.

Figure 31 .—Estimated volume of ponderosa pine killed annually on four units, Happy Camp-Lava Beds area, Modoc National Forest, California, during the period 1921 to 1935 inclusive.

(Pages 300a, 300b follow)

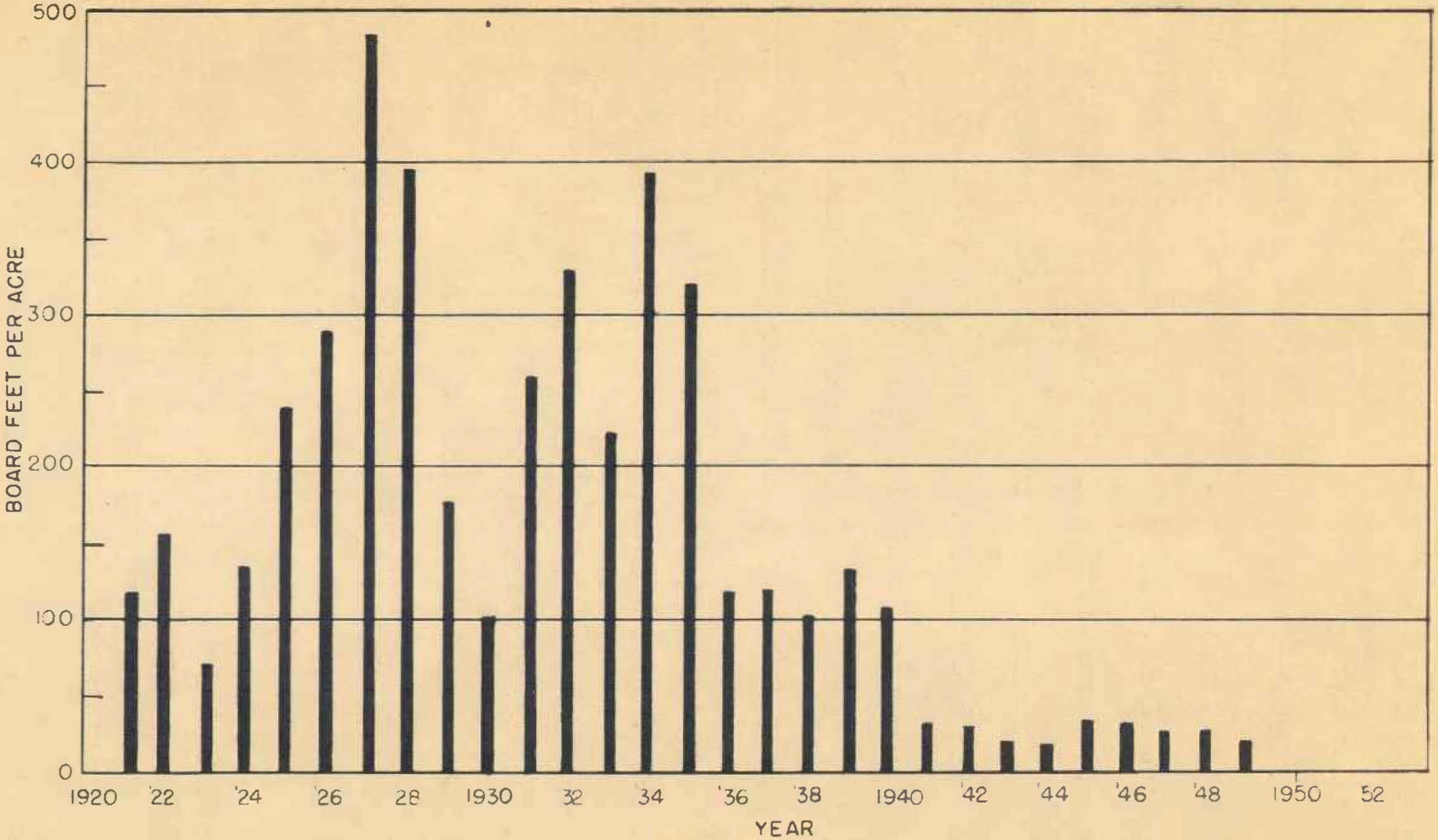


Figure 30.--Trend of western pine beetle infestation on virgin ponderosa pine sample plots, Happy Camp-Lava Beds Area, Modoc National Forest, California, 1921-1949

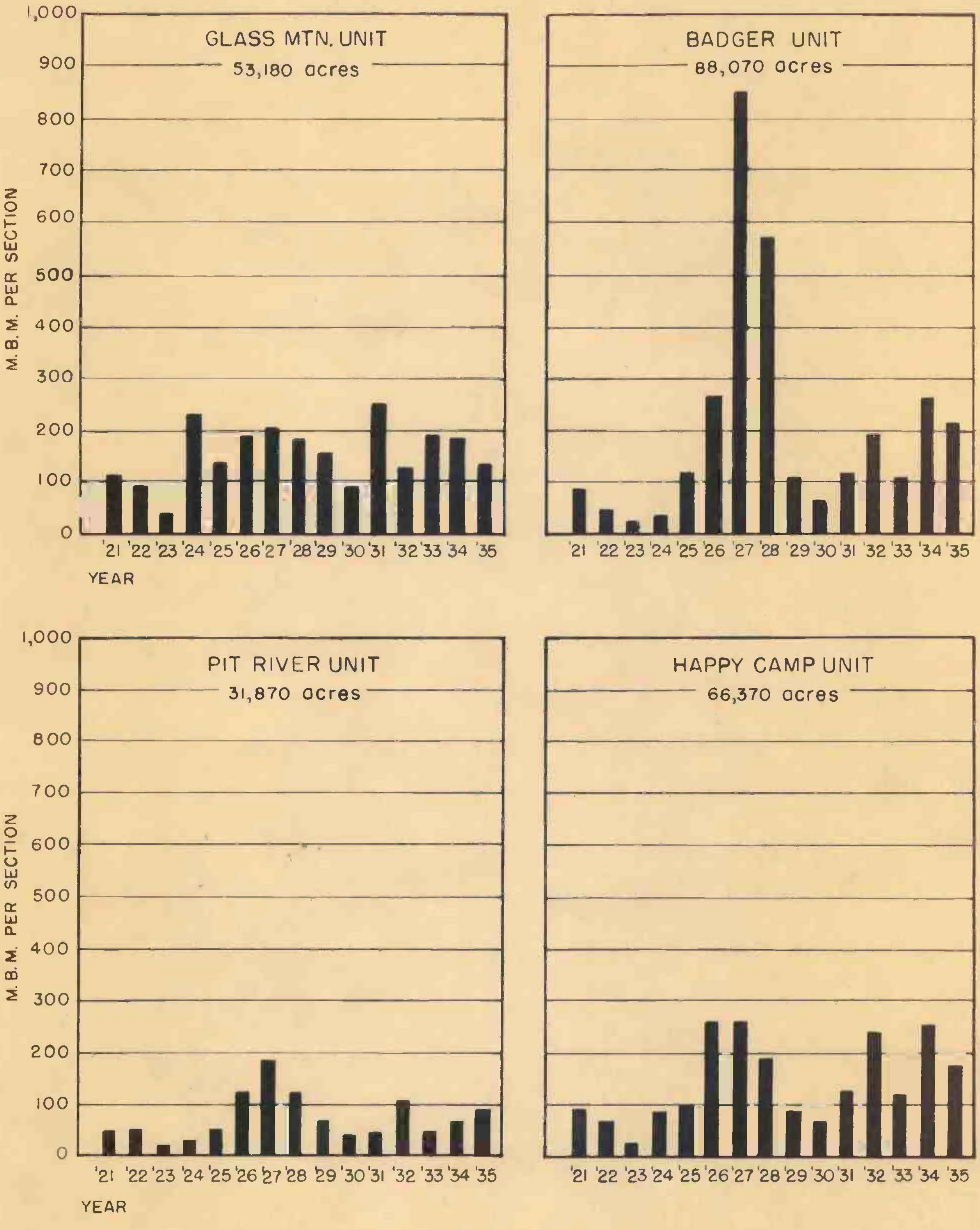


Figure 31 .-- Estimated volume of ponderosa pine killed annually on four units, Happy Camp-Lava Beds Area, Modoc National Forest, California, during the period 1921 to 1935 inclusvie.

These records were partially analyzed by Hall (U76), who made a study of the trends for the Modoc area, 1923-1938 inclusive, and the Lassen area, 1930-1938. The records for the Lassen area were available only for the second seven-year cycle, but the trend corresponded very closely with that on the Modoc. After presenting the loss figures in graph form, Hall stated: "This figure tends to show that there appears to have been 2 distinct cycles in losses since 1923. These appear by 7 years duration with the peak in both cases having been reached the fourth year following the low point in the cycle."

While the period 1921 to 1937 showed some evidence of two 7-year cycles, the period since 1937 gives little basis for support of the cycle theory. Like the Klamath Basin, this area since 1941 has been characterized by an extremely low level of endemic infestation. This low level may be due in part to the contraction of virgin stands due to the extensive selective cutting in adjoining stands, but is probably also due to the successive years of above average precipitation which have occurred since 1940.

The Westside Sierra Studies, 1912-1943

The longest period for which records are available of the annual fluctuations of bark beetle losses is found on the Sierra National Forest in the westside pine type near North Fork, California. The first records begin with control work which was started here in 1912. Loss measurements on selected sample plots were not started until 1929 so that an accurate record is incomplete for the entire period. However, control work by the Forest Service and special studies by forest entomologists were in progress during practically all of this period and enough data are available to construct a graph which reflects the high and low points in the infestation for 32 consecutive seasons. In discussing the trends in this westside area of the southern Sierras, Miller, Struble and Hall (U199) stated:

> "One characteristic of the beetle-caused loss record of the pine type of the Sierra is the irregularity of the annual kill, although there is some indication of a cyclic tendency during certain periods. If we look at the graph representation of the losses from 1912 to 1942, we find long periods of low loss levels below 200 board feet per acre interrupted by very brief periods when the loss rose above this level. Most striking of all are the years 1930-1932 when the loss rose sharply to a point in excess of 10 times the average for the preceding 19 years."

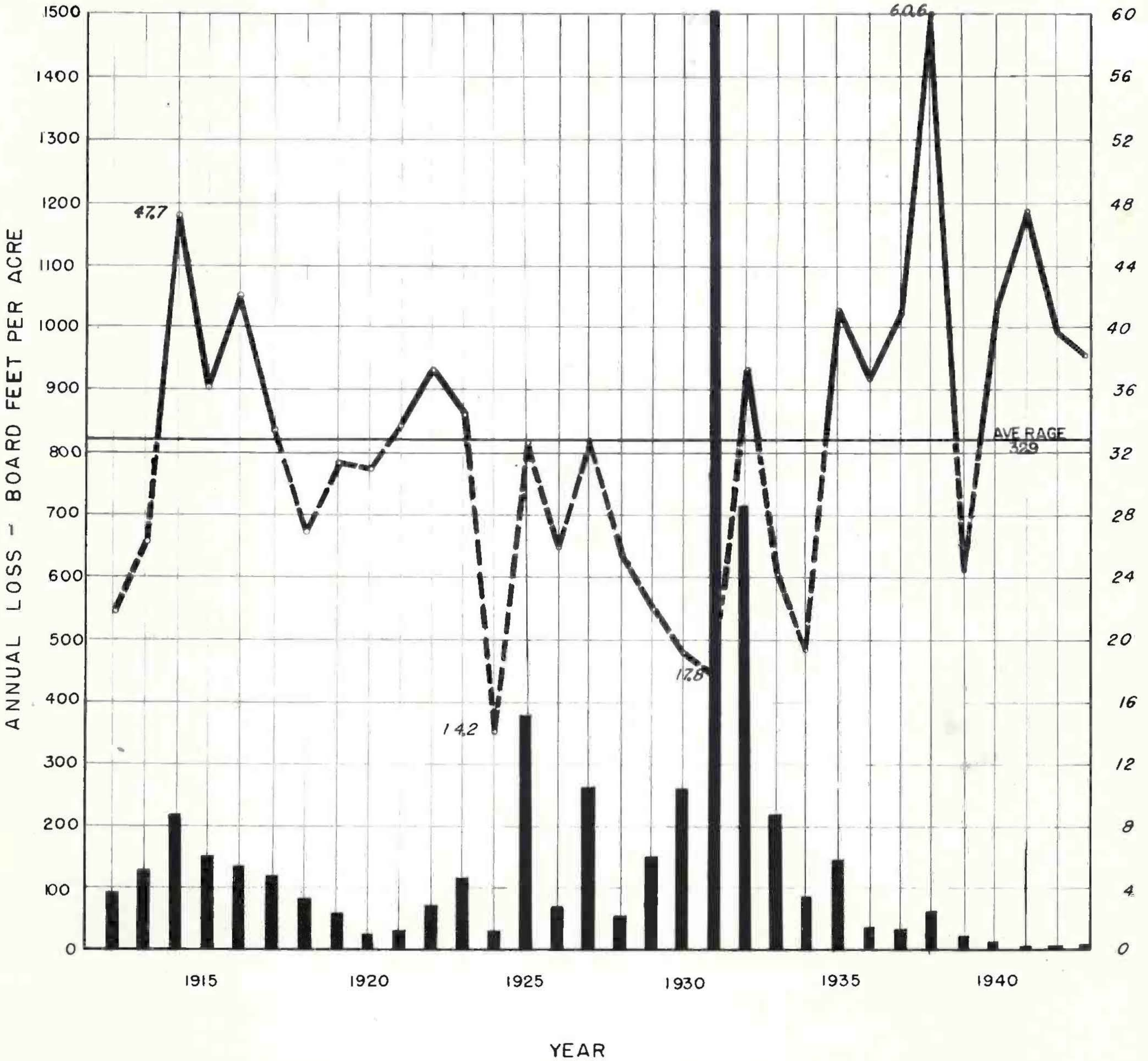
The graph referred to in this report (Figure 32) shows the annual board foot loss per acre, together with the seasonal precipitation.

Figure 32.—Relation between precipitation and pine mortality due to bark beetles, 1912-1943, Cascadel area, Sierra National Forest, California.

Much of the report quoted above is given over to the causes of these fluctuations. This is a very complicated field dealing with the ecological relations of the western pine beetle and an analysis of the factors involved will be taken up in Section IV of this review.

(Page 303a follows)

Figure 32.--Relation between precipitation and pine mortality due to bark beetles, 1912-1943, Cascadel Area, Sierra National Forest, California.



SECTION IV

ECOLOGICAL RELATIONSHIPS (FACTORS AFFECTING THE HOST TREE)

The biotic relationships which have been discussed in Section III included a long list of important factors which operate directly upon the western pine beetle to influence its abundance, - its fecundity, food requirements, temperature and moisture limitations, parasites, predators, diseases, and the role of associated insects in the beetle's economy. All of these and other factors may act either favorably or unfavorably upon beetle populations and up to a certain point determine the success or failure of the insects to survive and multiply.

But an equally important set of factors may be found in the insect-host relationships. The tree is also a living organism which reacts to its environment and attack by beetles. Certain trees offer strong resistance to attack, while others are easily overcome. These two contrasting conditions in the tree, known as resistance and susceptibility, are tied up mainly with the physiological conditions producing vigorous growth. The capacity of the tree to produce vigorous growth is influenced by such factors as heredity, age, crown size, position, site, soil fertility, moisture, climatic conditions, and silvicultural conditions in pine stands. All of these factors influence the epidemiology of the beetle by operating indirectly through its host plant.(20)

In this section we will review the studies which have been made of the tree's reaction to beetle attack, and the ecological and environmental factors which determine the tree's ability to resist such attack or succumb to it. These factors deal primarily with tree resistance or susceptibility.

THE EFFECT OF ATTACK UPON THE HOST TREE

The attack of the beetle upon its host tree represents a two-way biological relationship. Both are living organisms prior to the initiation of the attack, and both react to certain stimuli produced by the other. The beetle may select some particular tree, either by chance or attraction; and the tree, through such healing and growth processes as it is endowed with by nature, resists the attack until the beetle is either pitched out by resin flow or the tree succumbs.

Immediate Reactions of Living Trees to Attack

The Mechanical Injury and Resin Flow

The attacking beetle at first bores through the corky layer of outer bark causing no damage to living tissues of the tree. But it soon reaches the phloem layer where it finds the living cells that make up (1) the conductive tissues that transport soluble starches and sugars, (2) the storage cells that hold these materials until they are built into wood by the cambium, and (3) resin canals whose chief function seems to be the conduction and storage of oleoresin, known as the "pitch" that serves to seal over wounds. As the beetle further advances its tunnel, it enters the thin cambium layer but bores no deeper into the tree than to barely score the sapwood.

The effect on the tree of these first phases of the attack is apparently identical to the reactions produced by mechanical injury. The result is very much the same as would be expected if a hole was drilled through the same layers of plant tissues by a tiny auger. As the resin canals are severed, pressure is released and usually a copious flow of pitch is forced into the wound. Some moisture also seems to drain into the wound along with the pitch; but it is the flow of pitch that is the first response of the tree to attack and apparently constitutes its first and only line of defense against invasion by the beetle.

"Pitching Out" - an Indication of Tree Resistance

This pitch flow apparently causes the beetle no end of concern and irritation. If allowed to dry in the entrance hole, the gummy pitch gradually hardens and plugs up the opening. To prevent this, the beetle works the pitch out to the surface of the bark and builds the pitch-tube. Successful attack is not accomplished until the exudation ceases. A continuing abundant flow of pitch over a long period either results in death of the beetle or abandonment of the attack. This result, known as "pitching out," may be due to exhaustion of the beetle or to the toxic effects of the turpentine or resin acids that make up the pitch.

A few attacks on a vigorous tree will always pitch out, but concerted attacks over a large percent of the bark surface of the tree usually result in drying the sapwood and impairing the tree's ability to produce resin. When this occurs, attacks are successful. There are cases to be found of attacks that fail, either because of the strong flow of pitch in certain trees or because the beetles did not attack in sufficient numbers to overcome this pitch flow.

Considerable effort has been directed toward finding the basic factors that enable certain trees to successfully resist attack, while others do not. If resistance can be attributed to resin flow, then the differences between individual ponderosa pine trees may be related either to variations in the quantity of resins produced or to the quality or to both. That wide differences do occur in the composition of the resins from individual ponderosa pines has been established. Mirov (U201),who made a preliminary study of this phase of resin production in 1928 reported: "Some turpentining experiments by the U.S. Forest Service in California showed that the chemical composition of oleoresin from different specimens varied greatly."

That the amount of resin produced also varies greatly between individual trees is a matter of common observation, and this has been generally accepted as related to growth vigor. However, Mirov (U201) reported:

> "Usually considerable stress is laid upon the pitch yield of trees on the supposition that slow growing trees if attacked by bark beetles produce a smaller amount of oleoresin than fast growing trees, and thus are less resistant to attack... During the turpentining experiments, it was found that there is very slight, if any, correlation between growth rate and oleoresin exudation."

Insufficient work has been done to determine the actual effect of the various chemical substances in the pitch flow upon the attacking beetle. Studies that have been made seem to have by-passed the role of resins in the selection of trees by the beetle, and the relation of quality and abundance of pitch to the resistance of certain trees to attack.

The Effect Upon Transpiration and Growth Functions

As a successful attack becomes established, the egg galleries are extended through the phloem in a criss-cross pattern until the tree has been completely girdled. This phase of the attack effectively breaks down the circulatory system in that part of the tree. Water and food materials in solution can no longer be transported from the leaves down the main trunk. The effect upon the wood-building functions is therefore immediate and cambial growth soon ceases; but the foliage is still intact and obtains water for transpiration from the stored water in the stem. Consequently the needles remain green for some time after the attack is established. When the stored water is exhausted, the needles die. On the whole, the egg galleries alone produce an effect similar to that in a pine which has been girdled to the depth of the sapwood with an axe. But while mechanically girdled trees may remain green for as long as a year or two regardless of the injury to the inner bark, phloem, and cambium, beetle-attacked trees die much more quickly.

The girdling process of the beetle involves considerably more than the mechanical injury to the tissues. First the beetles in opening up tunnels into the phloem area allow air to dry out the sapwood cells beneath these tunnels. They also carry in the spores of a yeast which set up fermentations in the sugars of the phloem. These will be discussed later. Thirdly, a blue-stain fungus is introduced, either by the beetle or by wind-blown spores which find entrance into the egg galleries. This fungus attacks the sapwood and while it does not destroy the wood cells, it apparently blocks their capacity to conduct water to the foliage. As a final result of the combined work of the beetle and the blue-stain fungus, the needles are deprived of water, transpiration ceases, the needles lose their chlorophyll and turn straw color; and the tree, for all practical purposes, can be classed as totally and finally dead.

Period of Time Required for Beetles to Kill a Tree

The length of time required for a tree to go through this process of dying varies with the season, with the resistance of the tree, and with the amount of time required by the beetles to establish a complete attack. As pointed out by Keen (U126), the attack may extend over a long period of time, advancing gradually from the top of the tree downward; or the attack may be made simultaneously on the entire length of the main bole and become established within a week or so. In that case the tree dies rather rapidly depending upon whether the temperatures are sufficiently warm to produce rapid evaporation of moisture in the foliage and to stimulate development of the blue-stain.

Person (U229, U232) carried on intensive studies of the attack on a series of caged trees near North Fork, California, during the seasons of 1926 and 1927 and reported:

> "The difference in the period between attack and the death of the tree, for trees killed during the first flight period and during the second flight period, is very marked; an average of 42 days for the first and only 8 days for the second. Most of the difference is undoubtedly due to the much colder weather in the spring which makes the beetles less active... Another cause for this difference may be that the trees are much less resistant during July and August when the available moisture is low and the physiological processes are slower."

Death of Tree as Recorded by Dendrograph

In these studies, Person used two dendrographs of the type developed by Dr. McDougal of the Carnegie Laboratory,at Carmel California, to measure the effect of attack upon the growth. These instruments recorded with considerable amplification the changes in the diameter width of the tree at a point just outside the phloem area. During the seasons of 1926 and 1927 one dendrograph was used to record the daily and seasonal growth of a tree of normal growth behavior; the other instrument was used to record the behavior of a tree which died as a result of forced attack by the beetles.

The check tree showed a daily fluctuation in diameter thickness; there was a definite shrinkage during the warm hours of the day when transpiration from the foliage was rapid, and a swelling during the night hours and during cold periods of the day when transpiration slowed down. These diurnal changes in diameter width apparently reflected the amount of water maintained in the phloem cells of the main bole. At the same time the dendrograph recorded the gradual seasonal increase in ring width as the wood cells were laid on by the cambium.

On the attacked tree, growth behavior was quite similar to that of the check until the time that the attack was established. Person's report on this tree stated:

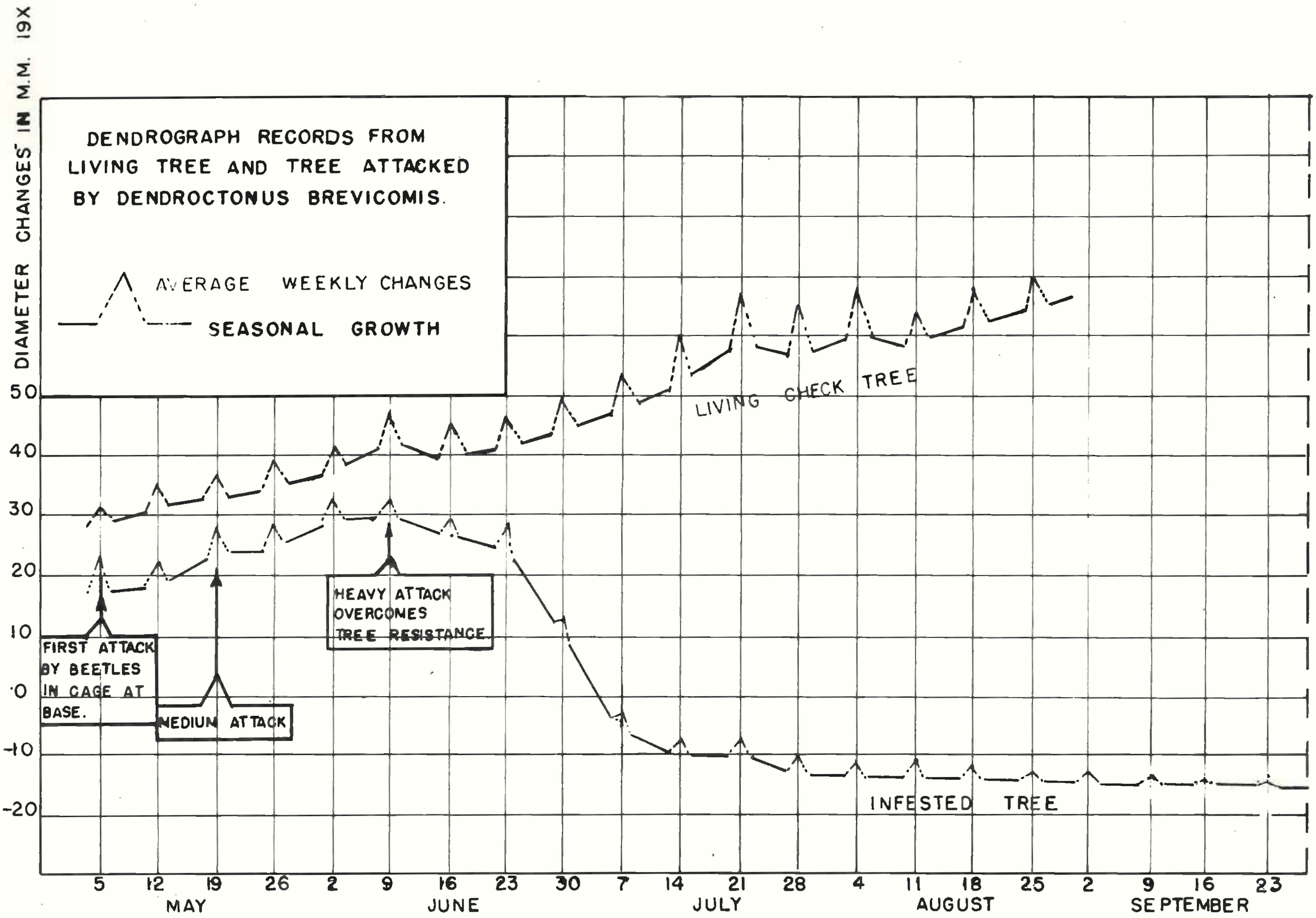
> "Early in June a very heavy attack was made and the tree was killed. This resulted in a rapid drying out and shrinkage of the phloem and sapwood which continued at a decreasing rate up until the end of the season. As the tree became drier and the needles ceased to function, the diurnal change in diameter became barely perceptible and the curve became almost a straight line."

The chart (figure 33) illustrating the growth curve of this tree shows increasing diameter growth from May 5 to June 9. During the period a light attack was made May 5 and a medium attack May 19 which failed to make any impression on the growth curve or the diurnal fluctuations in diameter. Following the heavy attack on June 9, shrinkage of the diameter began and was greatly accelerated from June 23 to July 14; after which the continued loss in diameter width was slight, but still perceptible. The diurnal fluctuations become much less pronounced after July 21, but were still perceptible until September 23. It was apparently Person's interpretation that the tree had been killed when the rapid shrinkage set in after the attack of June 9. This interpretation seems to be a sound one when we compare the growth curves of the attacked trees with those of check trees.

Figure 33 .-- Dendrograph records from living tree and tree attacked by Dendroctonus brevicomis.

(Page 312a follows)

Figure 33.--Dendrograph records from living tree and tree attacked by *Dendroctonus brevicomis.*



The Role of Micro-Organisms

The Blue-Stain Fungi

Identity.-- Soon after the egg galleries have been established, discolored areas appear on the surface of the sapwood which rapidly acquire a bluish-black color. These are caused by "blue-stain" fungi that are invariably associated with successful attacks of the beetles. A very considerable amount of work has been done to determine the relationship of these fungi to the rapid death of the tree and subsequent deterioration of the sapwood. According to Rumbold (108): "The blue-stain fungus growing from the galleries of Dendroctonus frontalis in eastern pines and D. brevicomis in the pines of California and Idaho has been identified as Cerotostomella pini." That this fungus is specific to these bark beetles and is introduced into the trees at the time of attack is born out by Rumbold's studies:

> "Many fungi were isolated from blue-stained wood of insect-infested trees, but as a whole only one fungus would be cultured from the stained area of a specimen collected when the tree had just been invaded by the bark borers."

Parts of the tree attacked.— In describing the general characteristics of this fungus, Rumbold states:

> "The fungus covers the wood beneath the bark with a black granular growth, which makes the wood look as though covered with coal dust. The inner bark also shows this growth mixed with particles of dried resin. Beneath the black streaks, the fungus grows in toward the heartwood. Hence a cross section of an infested sapwood branch has the appearance of wedges of stained wood extending from the bark to the center... A microscopic examination of the wood shows that the fungus first invades the parenchyma cells of the wood rays. The hyphae pass from cell to cell through the pits. As their number increase, the end walls of the ray cells are pushed out and later even the side walls are broken out by twisted strands of brown mycelium, which now fill the whole ray."

Relation to brood development of the beetles.— The first development of *C. pini* starting from the egg galleries in infested trees usually occurs in irregularly distributed spots; but if moisture conditions are favorable, it continues to spread through the sapwood. In time the entire cross-section of the sapwood becomes involved. The heartwood, however, is not attacked. That this increase in the volume of wood attacked by the fungus is well correlated with the advance in brood development of the beetle has been established by studies on a number of salvage logging operations where infested trees have been sawn into log lengths and graded.

Salman and Johnson (U266) reporting on 338 logs which were salvaged in 1935 by the Fruit Growers Supply Company near Sunsanville, California, summarized the percent of mill degrade due to blue-stains according to brood stages at the time the tree was felled:

"Relation of Brood Stages and Blue-stain Deduction.

Number Logs	Brood Stages	Average blue-stain deduction %
54	Attack, parent adults, eggs, young to half-grown larvae	9.6
52	Young to full-grown larvae.	23.7
232	Full-grown larvae, pupae, new adults, abandoned.	47.1"

Blue-stain must be expected in insect-killed trees even though salvage is rapid (U305), but the stain percentage should not be high within two or three months after attack. Although the heartwood is not affected, it makes up only 2.5 of log volume, in typical eastside ponderosa pine, so that the sapwood condition is the dominant factor in considering salvage. In general, summer brood trees which dry out quickly have much less blue-stain, than winter brood trees.

Role of blue-stain in rapid dying of trees.— Craighead (24) advanced the theory that the blue-stain fungus is responsible for the much more rapid dying of the tree after attack than would be expected as a result of mechanical girdling by the egg galleries. He suggested that this might be accomplished "by some toxic secretions of the fungi destroying the living ray tissues of the main stem or affecting normal functioning of the leaves in transpiration." Nelson and Beal (94) in experiments with *Pinus taeda* report that blue-stains inoculated into trees killed them without the aid of bark beetles, apparently by the complete blocking of conduction in the sapwood. Caird (16,145) found that the beetle's mining action alone is sufficient to desiccate the host. However, no work seems to have been done to determine whether the western pine beetle is dependent upon the action of the fungus to accomplish rapid killing of attacked trees. It is generally accepted that *C. pini* does not attack and kill trees unless it is introduced by the beetle; on the other hand, it has not been demonstrated that the beetle can successfully attack and kill trees unless it is accompanied by the fungus. However, the association of the organisms is so constant and universal that the relationship appears to be more than accidental or casual.

The Yeasts

Identity.-- Much less is known about the behavior and functions of certain yeasts associated with the attack of the western pine beetle than for the blue-stains. Person (105) first called attention to the probable role of a yeast considered to be a *Torula* found associated with the western pine beetle, (later determined as *Saccharomyces pastori* (Holst)).

> "It was possible to make pure cultures of this organism, and some experiments were conducted on its fermenting capacity. Although some other yeasts, bacteria and fungi were occasionally present in the cultures, the yeast was by far the most abundant and only organism apparently always present on the larvae and new adults of the beetle. It was found that inner bark inoculated with this yeast was definitely attractive to the western pine beetle."

Struble (U284) investigated the question of whether this yeast was also found in the intestinal tract of the beetle. He cultured the intestinal tracts of fully grown larvae in an agar-agar consisting of 10 grams of peptone, 2 grams of potassium phosphate, 0.5 grams magnesium sulfate, 20 grams of agar-agar, and 1000 cc. of boiled rice starch. Enough citric acid was put in to produce a pH of 4.8. All cultures produced a yeast. Struble concluded that "yeasts are evidently the normal organisms of the *Dendroctonus brevicomis* digestive tract, both in the larval and the adult stage of development. Fungi are occasionally present."

Holst (39) described a new species of yeast, *Zygasaccharomyces pini*, which was found associated with *D. brevicomis* from the western states and *D. frontalis* from the southern states. He also noted "some anascosporous, mycelium-forming yeasts were also frequently present." He was unable to find any evidence of direct relationship between the yeast and the beetle.[12]

Rumbold (109) does not mention any studies of yeasts cultured from the western pine beetle, but states that:

> "The two types of yeasts *Zygosaccharomyces pini* and the anacosporus yeasts that were regularly associated with *Dendroctonus monticolae* and *D. ponderosae* are those found with other species of bark beetles. They appear to be widespread in the forests of this country. They are regarded as of secondary importance in causing the death of insect-infested pines."

Probable function of the associated yeasts.— Jeffrey (U103, U104) made a chemical analysis of the concentration of certain sugars in the inner bark of trees attacked by the western pine beetle and concluded that the changes that take place soon after attack are the result of action by yeasts.

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[12] Further work was done in 1952 and 1953 by Moshe Shifrine, graduate student of the University of California, in cooperation with the Berkeley Forest Insect Laboratory in regard to yeasts associated with *Dendroctonus* and *Ips*. The most common yeasts associated with *Dendroctonus monticolae* in ponderosa pine were *Hansenula capsulata*, *Candida sylvicola*, *C. parapsilosis*, and *Saccharomyces pastori* (*Zygasaccharomyces pini* Holst.). In ponderosa pine, practically the only yeast found associated with *Dendroctonus brevicomis* was *Saccharomyces pastori* (Holst).

> "In recently felled trees, before attack, there is evidence of an increase of levulose and a decrease in sucrose. When trap trees are attacked by D. brevicomis the reducing sugars in the inner bark, especially levulose, increase and the sucrose decreases rapidly. This is followed by a decrease in all sugars, which is especially rapid, close to the beetle galleries. The decrease is probably the result of abnormally high cell respiration, and of fermentation due to microorganisms introduced by the beetle... When a tree is felled or injured (and becomes attractive to the beetles) there is an increase of levulose and a decrease of sucrose such as would probably be associated with fermentation."

On the whole the small amount of information which has been collected regarding these yeasts associated with western pine beetle attack indicates that they contribute to deterioration of the tree only to the extent of breaking down certain materials in the phloem as the tissues change from the living to the dying condition. Their principal significance, as pointed out by Person (105) lies in the production of esters whose odors seem to attract the beetles during the period of attack.

Deterioration of Beetle-Killed Trees

Once the growth processes cease in a tree that has been attacked, changes set in that result in its deterioration and ultimate decay. The foliage dies quickly and passes through a series of successive color changes; the dead needles finally fall, leaving the limbs bare; woodborers and rots attack the sapwood and bring about its disintegration; the bark loosens and falls; and in the end the tree becomes a snag which may soon fall or may stand for years as a bleached "ghost tree." All this chain of developments requires a period of years and the various stages of deterioration correlate fairly well with elapsed time after the tree dies.

Color Phases of the Dying and Dead Foliage

The most visible effect of successful beetle attack on a pine tree is registered by the foliage. The succession of color changes that takes place corresponds to, and somewhat resembles, the color phases of broad-leaved trees as they take on their autumn foliage.

The presence of a bark beetle infestation in a pine area is easily recognized from a distance by the off-color appearance of infested and recently abandoned trees. By the simple visual method of viewing an area, an impression can be gained of the status and severity of an infestation. The interpretation of the color phases of beetle-killed trees has, therefore, been widely used as an index to bark beetle conditions in all detection surveys.

Terminology.— According to Hopkins (42), "The first evidence of attack on living trees is the presence of pitch-tubes on the trunks, mixed with reddish borings around the base of the tree. Later the fading yellowish or reddish condition of the foliage is conspicuous evidence of the beetle's work."

Hopkins was the first to define the color phases of infested trees which have been commonly used in all survey and control work. The term "tops" was used in connection with the color terms designating the overall appearance of the crown.

> "Fading tops: noticeably paler green of the foliage.
> Sorrel tops: the yellowish foliage of trees dying from attack.
> Red tops: color of the foliage after tree is dead and usually after the broods of destructive beetles have emerged from the bark. This reddish brown of the adhering pine needles may prevail for a year or more after the trees are dead.
> Black tops: condition of dead trees after all of the needles have fallen and 2 or more years after the beetles have left them."

Relation of color phases to brood development.— Keen (U128) found a certain amount of correlation between the development of the color phases and the various stages of brood development. He also found that this relation varied considerably with the time of year. These relationships he illustrated by graphs with the following general summary:

> Fading: "In general a tree fades soon after the larvae hatch and at about the time they enter the outer bark. Trees of the overwintering generation, however, do not fade as a rule until the first warm weather in spring and before pupae form."
>
> Sorrel: "As a rule trees turn sorrel at about the time of maximum pupation or the first forming of the new adults."
>
> Red: "Trees generally turn red about the time of maximum emergence of the beetles."
>
> Black: "Completely abandoned by the western pine beetle; wood borers and secondary insects in the wood."

Deterioration of foliage.-- During the 1933 season, Buckhorn (U38) charted the change of color phases for a series of trees attacked in 1932 on the Ochoco area in eastcentral Oregon. He showed that up to the last of May 1933 following the overwintering period, 90 percent of the 1932 first generation trees were sorrel, the remainder still green. For the partial second generation trees, 70 percent were fading, and 30 percent were still green. For the partial third generation trees attacked late the preceding fall, only 40 percent had faded.

During June and July the color phases in all trees advanced rapidly and by November 1 practically all had reached the red and dull red stages. From the first of September on, the loss of needles was noticeable and the trees went into the second winter with about 35 percent of the foliage fallen.

The red color phases may be broken down into "bright red" and "dull red" phases. The bright red phase identifies trees that have not passed through a winter, while the dull red phase applies thereafter to the weathered appearance of the needles.

The red phases last for a prolonged period, the length of time depending somewhat upon weather conditions to which the abandoned trees are exposed. Winds and sleet hasten the fall of dead needles. The period that trees remain in the red phases has been found to vary with locality and region, but in general there is a progressive fall of needles after the first year with some trees retaining 10 percent or more of needles for a period up to five years. (U75).

Records taken on four 640-acre sample plots in southern Oregon in 1935 show 15 percent of needles fallen in the first year, 38 percent of trees with needles fallen after two years; 62 percent after three years; 94 percent after four years; and 99 percent after five years. If all trees with red needles are counted, they equal an average of 1.8 years of loss.

After dead trees have dropped their needles, they are considered to be in the "black-top" stage, even though a few weathered, inconspicuous brown needles are retained. Snags in the black-top phases, before bark has started to fall, may be anywhere from 1 to 13 years old. A count of all such snags plus red tops has been found to average about 6.7 years of loss.

The next older class of snags with the bark slipping have been called "yellow-tops." They may be anywhere from 2 to 15 years or more old. Checks on plots [sections] where past loss has been marked show that a count of "yellow-tops" plus black and red tops, will average about 8.3 years of loss.

The oldest class of snags, with most of the bark fallen and the wood bleached gray white have been called "white-tops" or "buckskins." Snag counts show these snags to be from 5 to 30 years or more old. A count of all snags including red tops, black-, yellow-, and white-tops has been found to equal about 9.6 years of loss. A rule-of-thumb of counting all snags as equal to about 10 years of loss has been used in cruising timber in the interior ponderosa pine type for some years, based on these snag studies.

On the whole, the color phases of beetle-killed trees which are of greatest significance in appraising current bark beetle infestations in survey and control operations are the early fading and sorrel stages. Beyond these stages, the trees are mainly abandoned and the red and black phases are of importance only in estimating past losses.

Falling of Bark

The falling of bark has also been used as an indicator of the rate of deterioration of a beetle-killed tree. Hall (U75) states that there is comparatively little loss of bark up to the fifth year after death; at the eleventh year the average loss of bark is approximately 50 percent and at the sixteenth year the loss is approximately 90 percent.

From recruising a series of check plots in southern Oregon, Keen found that the rate of bark falling was exceedingly variable. Trees with all bark intact might be anywhere from 1 to 13 years old and average 5½ years old. Those with bark slipping might be 2 to 15 or more years old and average 11.2 years. While those with more than 75 percent of bark gone might be 5 to 15 years or more old, the average is about 25 years.

Deterioration of the Main Bole

The destruction of sapwood and heartwood that goes on gradually after the tree is abandoned by the beetles is accomplished by the combined action of weather, insects, and fungi. The causes that bring about the deterioration of the merchantable part of the tree have been given some study, primarily because the rate of deterioration is quite important to the possibility of utilizing the lumber values in beetle-killed trees.

Influence of weather factors.-- The role of weather in the deterioration of bark and wood has not been studied, but it cannot be altogether disregarded. Climatic conditions regulate to a considerable extent the amount of water in the wood of dead trees and it is upon this moisture that rots are dependent for favorable conditions for development. Beetle-killed trees in moist sites appear to rot rather quickly while those that are found in dry climates have a tendency to check badly due to rapid drying out. Both conditions destroy the merchantable quality of the wood and are factors in the process of deterioration.

Insects.-- The western pine beetle does not attack the wood and is only indirectly a factor in the deterioration of the main bole. Wood borers, however, soon follow the beetle and not only destroy the wood, but help the development of rots.

Ambrosia beetles.-- While the lower trunk of the freshly killed tree is still fairly moist, the sapwood and later the heartwood is invaded by ambrosia beetles or "pin-hole" borers which plant fungi in their galleries on which their larvae feed. These holes apparently admit the spores of wood-rotting fungi and hasten wood decay.

ich ones?

Trypodendron ponderosae Sw. is one of the most common species found attacking the base and lower eight to ten feet of the trunk of beetle-killed ponderosa pines that are moist or show "sour sap" at the base. According to Buckhorn (U38), the galleries penetrate the sapwood and heartwood and branch considerably. "Broods attack the trees soon after they are killed by bark beetles and continue until late in the fall and start again with favorable spring temperatures. Brood was found overwintering in the adult stage mostly in the newly formed galleries,but a few were wintering in the old brood trees and at the base of trees under loose bark scales." The peak emergence occurred from October 2 to December 7. Apparently there is only one generation a year.

Gnathotrichus retusus (Lec.)is also a common species of shot-hole borer found breeding at the base of moist ponderosa pines. They make numerous small pin-holes in the sapwood. The galleries usually have one or more horizontal branches following an annual ring and from these larval "cradles" are constructed both above and below. The brood overwinter in the adult and larval stages in both old and newly beetle-killed trees. Adults were also found hibernating at the base of trees under loose bark scales from the ground line to several inches below ground and on the roots. Other species of ambrosia beetles may occasionally be found doing similar work.

When the wood is fairly rotten and punky, another pin-hole borer, *Xyleborus scopulorum* Hopk. appears. This species makes no cradles, but frequently branched horizontal galleries in which the larvae work end to end.

Sapwood weevils.-- Small black weevils, *Cossonus ponderosae* V.D.,6 mm. long, and *C. crenatus* Horn,5 mm. long, are found under the bark of killed trees within a year and start working on the blue-stained sapwood. The small white curled larvae make small round, mostly horizontal pin holes in the sapwood to a depth of 3 inches.

Rhyncolus oregonensis Horn. are small dark reddish brown weevils, 4 mm. long, which also are found under the bark soon after the tree is killed. The adults construct galleries radially and horizontally deep in the sapwood. Ten or more adults may be found in a single gallery working side by side, particularly in very dry wood.

Round-headed borers (*Cerambycidae*).-- A number of round-headed borers are attracted to ponderosa pines recently killed by the western pine beetle and the larvae on hatching start penetrating the sapwood and heartwood. The most important species in this respect are. -

Asemum atrum Esch. may be found in the larval stage, mining the moist sound sapwood of trees dead for from 2 to 7 years or more, and extending their oval mines into the heartwood. The galleries in the wood are usually packed with red frass, except for the pupal portion which extends to near the surface of the bark. *A.nitidum* Lec. is a larger species which does similar work. *A. mokelumne* (Csy) is another species, which is the one most commonly found in the wood of ponderosa pine.

Ulochaetes leoninus Lec. may be found laying eggs on ponderosa pines a year after being killed. The larvae will be found working in the wood particularly at ground line and in the roots for many years afterwards. It is undoubtedly an important species in undermining pines and causing them to fall.

Ergates spiculatus Lec. Larvae of this large wood borer may be found within three years after death of ponderosa pines, working in the sapwood and into the heartwood. It continues to work in old trees and stumps until the wood is completely riddled with its very large tunnels which are oval and an inch or more in largest diameter.

Strangalia plagifera (Lec.). Larvae of this species work in old decaying sapwood from the surface to four inches into the wood. Pupae form in cells three inches under the surface. This species is common in the older pine snags.

Many other species of roundheaded borers may be found in old decaying wood of bark beetle-killed pines.

Flatheaded borers (Buprestidae).— A few species of flatheaded borers are also found working in beetle-killed pines. The most common species include:

Chalcophora angulicollis Lec. is a large species which lays its eggs on the bark of dead pines about two years after they are killed, and the larvae work into the sapwood. By the fifth year larvae will be found from the surface of the wood into the heartwood and down into the roots.

Buprestis aurulenta L. works in the pitchy wood of fire scars and at the base of old snags. The larvae develop slowly and may be found infesting this wood for many years.

Other flatheaded wood borers include Buprestis laeviventris (Lec.) and Dicerca tenebrosa (Kirby).

Other wood borers.—

Rushia californica (Fall) is a common species of wood borer found under the surface of hard, dry sapwood of snags over two years old. The larvae are narrow, white, about 12 mm. long with two prominent hooks on the rear end. They make small flattened oval mines running in all directions, but mostly vertical, partly filled with powdery boring dust and partly open. They occur down to but not below the surface of the ground.

Phellopsis porcata (Lec.) ~~The~~ adults are large, rough, brown beetles. Larvae make long winding vertical tunnels packed with frass in the wood of snags three or more years old.

Termites.— The dampwood termite *Zootermopsis nevadensis* (Hagen) is commonly found attacking the damp sapwood of pine snags. Also the subterranean termite *Reticulitermes hesperus* Banks. is often very active in destroying the sapwood of old pines. They also continue into the heartwood of the older snags.

Fungi causing stain and wood decay.— Wood-staining fungi are the blue-stains *Cerotostomella pini* and others (discussed on page 313), and a yellow stain of an undescribed fungus, studied by Wagener (U305). Patterson (101) found in southern Oregon that the amount of blue-stain varied in individual trees according to the amount of sapwood, which in general was 40 percent of the merchantable volume of beetle-killed trees. During the first season after attack, deterioration of the lumber values in the tree is confined chiefly to a degrade due to bluing of the sapwood. Blue-stain is usually well developed throughout the sapwood by the end of the first season.

Wood that has been blue-stained still retains much of its structural properties and can be utilized, but because of its discoloration is graded much lower for commercial uses than lumber that has not been attacked. Under some conditions blue-stained wood has been able to command high prices when put to special uses.

Sap rot.-- Wagener (U305) found that wood-destroying fungi (unidentified) may gain considerable headway in the sapwood the first year after the tree is attacked. "Once established the decay appears to develop rather rapidly from narrow longitudinal streaks into irregular patches. The extension takes place along the surface of the sapwood, no doubt aided by the activities of secondary insects under the bark. From here it spreads somewhat more slowly and irregularly toward the heartwood."

The red belt fungus, Fomes pinicola is the most common cause of rot in insect killed ponderosa pine. It first shows up as a faint yellowish or brownish stain. In the advanced stage it reduces the sapwood and heartwood to a light reddish brown crumbly mass which has a tendency to fracture into cubes. This rot is an important factor in the ultimate decay of beetle-killed snags.

Polyporus volvatus develops in the outer sapwood while western pine beetle brood are still in the tree and its fruiting bodies develop thorough emergence and ventilation holes after the beetles emerge. These fruiting bodies are most plentiful during the season following emergence. This fungus causes a soft grayish rot of the sapwood which often progresses very rapidly.

Progress of combined rots.— In 1922 Boyce (7) made a study of the deterioration of treated trees on an insect control project near Klamath Falls, Oregon. He found that while the heartwood of ponderosa pine resisted rots considerably longer than the sapwood, it also decayed in time.

> "Deterioration is very rapid and is caused by decay, particularly the very rapid decay of the sapwood followed more slowly by the breaking down of the heartwood. The resulting loss is so high by the end of the second season that felled trees must be utilized by the beginning of this time or else the volume of merchantable wood is so small that it is of little commercial importance."

Boyce found that the percent of cull two years after the infested trees had been treated amounted to 60 percent; this percentage increased progressively with each succeeding year until by the seventh year 92 percent of the wood material was valueless.

Patterson (101) in reporting on a salvage operation of beetle-killed ponderosa pine on the Modoc National Forest of California in 1928, showed the following percentage of merchantable volume salvaged by seasons:

Season of attack	Percent Blued	Percent of merchantable volume salvaged in 1928
1927 winter brood	43 %	100 %
1927 summer brood	39	86.4
1926 winter brood	37	73.2
1926 summer brood	50	47.7

No tree dead longer than two years contained enough merchantable stock to defray expenses of logging.

Brundage and Orr (12) discussed the selling values of lumber obtained from infested trees salvaged on an eastside pine area in 1935.

How Long Do Beetle-Killed Trees Stand?

The end result of the processes of deterioration in standing beetle-killed trees is the breaking down of the wood, particularly at the ground line and in the main bole so that the snag finally falls and its ultimate disintegration takes place on the ground. Keen (64) made a study of the period that these beetle-killed trees remained standing on one 640-acre check plot in Modoc County, California. This early study was supplemented by a recruise of snags still standing on three 640-acre check plots in 1932, on three other 640-acre check plots in 1935, and the Modoc plot was again recruised in 1949. He found that the natural falling of ponderosa pine snags of the interior type of southern Oregon and northeastern California follows a rather consistent pattern. A high percentage of these snags remains standing for the first five years. Then as the butts become riddled with wood borers, termites, and wood rots, the trees fall in rapid succession. Between the fifth and twelfth year the bulk of the snags go down. After the twelfth year, the drop out slows down and the more resistant snags of larger diameter remain standing for many more years. Ten percent of snags killed for 17 to 30 years were found still standing when the Modoc plot was recruised in 1949; while 28 percent remained of snags in the 40 inch d.b.h. class and over. It was found that snags stood longer on dry pumice soils than on the more moist clay and loam soils.

It is a matter of observation that trees with pitchy butts, trees standing on dry sites, and those charred and "case-hardened" by fire are the last to succumb to the process of decay, and the studies show that it is these that make up the last ghost trees still standing in areas where epidemic occurred years before.

HOST TREE RESISTANCE AND SUSCEPTIBILITY

There are two opposing theories as to how western pine beetles find suitable host trees to attack. One theory advanced by Person (105), already discussed, is that certain susceptible trees throw off odors or other attractive substances which draw a few beetles to these trees, which are then attacked. This attack in turn sets up additional attractive influences which bring in additional beetles to assist in overcoming the trees.

The other theory is that, at least as far as the first beetles are concerned, attack on trees is merely a random chance. (U49). Beetles flying through the woods attempt to attack many trees. On resistant trees, these attempts fail due to the quantity of oleoresin produced by such trees and the attacking beetles are pitched out. But on susceptible trees, little or no resistance is offered and the attacks succeed. Once the initial attacks are started, other beetles are drawn to the scene and lend their aid and support until the tree is overcome. This becomes a focal center and beetles may continue to come until a group of trees are killed around the first or "key tree."

Neither of these theories have been demonstrated but in either case we do know that certain trees are more susceptible to attack than others, regardless of how the beetles happen to find them.

Relation to Tree Conditions

Physiological Factors

Studies of physiological conditions of the tree have been concerned with growth and other functions which were considered essential to the plant in resisting beetle attack. In the previous section/is an account of the breaking down of the vital functions of a ponderosa pine under a successful attack. Weakening of the tree's resistance was manifested by slowing down of the resin flow, reduction of transpiration, gradual drying of the tissues, and finally complete stoppage of all growth functions. The capacity of the tree to maintain these functions, under beetle attack or other adverse conditions, is obviously a measure of its resistance.

Growth.— Growth rate as a possible indicator of tree resistance and susceptibility was one of the first factors given detailed consideration. The first studies on growth rate in relation to western pine beetle attack were those started by Person and Keen as a result of suggestions made by Dr. Craighead and Munns in 1923. From 1924 to 1928 Person carried out a series of studies on the Sierra National Forest to determine whether the mortality of pines from western pine beetle attack was related to such factors as growth rate, quality of site, tree diameter, and size of crown. He considered growth only as it was expressed by ring-width measurements (average ring width in last inch of radial growth) in basal increment cores. Basal increment cores from beetle-killed and living trees were collected by Person from the westside type of the Sierra National Forest, and a similar large series of cores were collected under Keen's supervision from survey plots representing eastside type in southern Oregon and northern California. The growth rates were measured and compared between trees of the same diameters growing on the same sites. The results of these studies were reported by Person (104, U228, U233) who concluded that:

> "There is a definite selection of the slower-growing trees. In comparing attacked and unattacked trees of the same diameters on the same sites, the beetles selected the slower-growing trees in 75 percent of the cases. In 91 percent of the trees attacked, the growth rate was below 2 mm. annually."

Struble (U294) further confirmed this relationship in a study of the Cascadel plot, Sierra National Forest, California. For 230 trees which died during the period 1917 to 1926 out of a total stand of 1362 trees, the selection by growth class favored the slow-growing trees. This relationship is shown in Figure 34.

Figure 34.--Percent of trees killed by growth classes, Cascadel Area, Sierra National Forest, California, 1917-1926.

The first published statements concerning this work by Craighead (21), Miller (85), Person (104), Evenden and Keen (26) all reported that it is the slower-growing trees which are most frequently killed by the western pine beetle. What these authors meant by "slow growing" was not defined in any of these publications, but the observations and data upon which these statements were based were concerned only with the basal radial increment of the main trunk.

These early studies were followed by a tremendous amount of increment core growth studies in other areas. In 1924 Keen began the collection of cores and data on climatic conditions in eastern Oregon which culminated in his analysis of climatic cycles and tree growth rates in eastern Oregon (68) (see p.400). This showed that radial growth was correlated with precipitation and that drought conditions and slow tree growth during the period from 1917 to 1937 was undoubtedly an important factor contributing to heavy timber losses from the western pine beetle during this period.

(Page 337a follows)

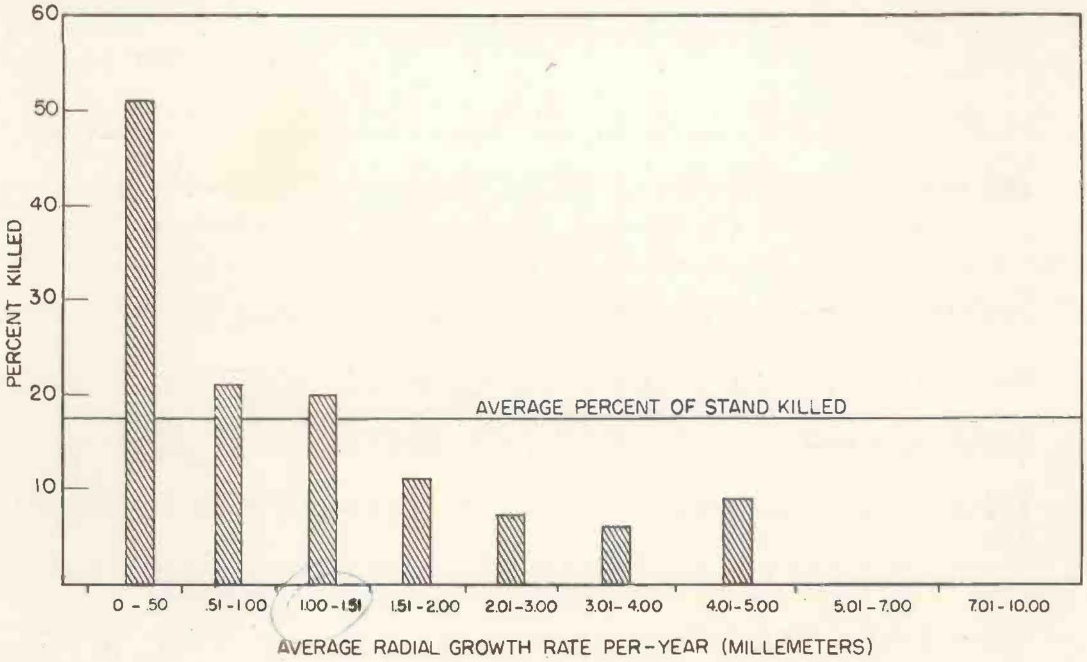

Figure 34.-- Percent of trees killed by growth classes, Cascadel Area, Sierra National Forest, California, 1917-1926.

The resistance of vigorous, fast-growing trees to western pine beetle attack has been demonstrated not only by the lack of susceptibility of young and dominant trees under natural forest conditions but also by caging experiments in which attempts have been made to kill the trees by induced attacks of the beetles.

Miller (U189) describes an experiment on the Sierra National Forest in 1925 which involved forced attacks by D. brevicomis on two trees of widely contrasting growth rates. The basal ten feet of each trunk was enclosed in a screen cage and quantities of infested bark placed in each cage so that the emerging beetles had no choice of attack, except on the tree with which they were enclosed. The results can best be described by the following table.

	Tree # 1 (fast growing)	Tree # 2 (slow growing)
Diameter breast high	36"	28"
Height	120'	110'
Crown class	Dominant	Intermediate
Crown form	Pointed	Flat
Crown length	Long	Short
Number rings in last inch of radial growth	5	64
Width of 1924 ring	2.30 mm.	.25 mm.
Total number adult beetles emerging in cage August 27-September 20, 1925	14,559	8,373
Attack on bark surface within cage August 27-Sept. 20	430	645
Attacks outside of cage for 2½ feet above cage top	20	175
Final result	No attacks on mid- or upper bole. Tree survived.	Entire bole attacked. Tree succumbed.

Not only was the slow-growing tree attacked and killed, but enough beetles were drawn into this center to attack and kill two adjacent trees. However, the great force of beetles liberated in the cage with the vigorous tree (#1) were quite unable to overcome its resistance and attract beetles in any numbers above the cage.

The following year Person (U229) carried out similar tests on a more extensive scale. Another attack was forced on the same fast-growing tree (#1) with the same result - the tree still resisted the beetles and had suffered no apparent setback in growth as a result of the attack of the preceding year (Figure 35). In addition, Person caged four more trees; one of these was rated as fast growing, one as medium, and two as slow growing. All four of these trees were successfully attacked and killed by the beetles, but it required more beetles a longer time to kill the fast-growing tree of this group. Person pointed out that "the period between the first attack and the date on which the tree was overcome was over twice as long for the fast-growing tree." Also, "the amount of pitch given off in resisting attacks was over twice as large on the basal 3½ feet of tree #3 (fast growing) as on tree #4 (slow growing)." Person concluded from these experiments that:

> "Yellow pine trees vary in their resistance to *D. brevicomis* attacks. The data so far secured indicate that the resistance of a tree varies roughly with the growth rate; other conditions being equal. The fast-growing trees offer the most resistance, the slow-growing trees the least. Very fast growth, thick bark, and large heavy crowns are evidently associated with this resistance."

Figure 35 .—Type of cage used to test western pine beetle's ability to attack and kill a fast growing ponderosa pine. Cascadel Experiments, 1926.

(Page 339a follows)

Figure 35.-Type of cage used to test western pine beetle's ability to attack and kill a fast-growing ponderosa pine. Cascadel Experiments, 1926.

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In analyzing the variation in average number of western pine beetle attacks per square foot with ponderosa pine growth conditions on the Jenny Creek area of southern Oregon during the ten year period, 1917-1926 inclusive, Keen (U138) found a direct correlation between number of attacks and radial growth rate (Figure 36). When the growth ring was narrow for a certain year, fewer beetles attacked the bark surface; when the growth ring was wide, indicating vigorous growth for the year, it took more beetle attacks per square foot to kill trees. This shows how growth vigor of trees is essential in producing resistance of pines to bark beetle attack.

Figure 36.--Number of attacks per square foot of bark surface in relation to average annual radial growth of ponderosa pine. Jenny Creek area, southern Oregon, 1917-1926.

That the relationship between growth rate and selection is not fixed but varies according to the intensity of the infestation and the availability of slow-growing trees in the stand was brought out by further work by Person in 1927-28. This was expressed in Person's report (U233) as follows:

(Page 340a follows)

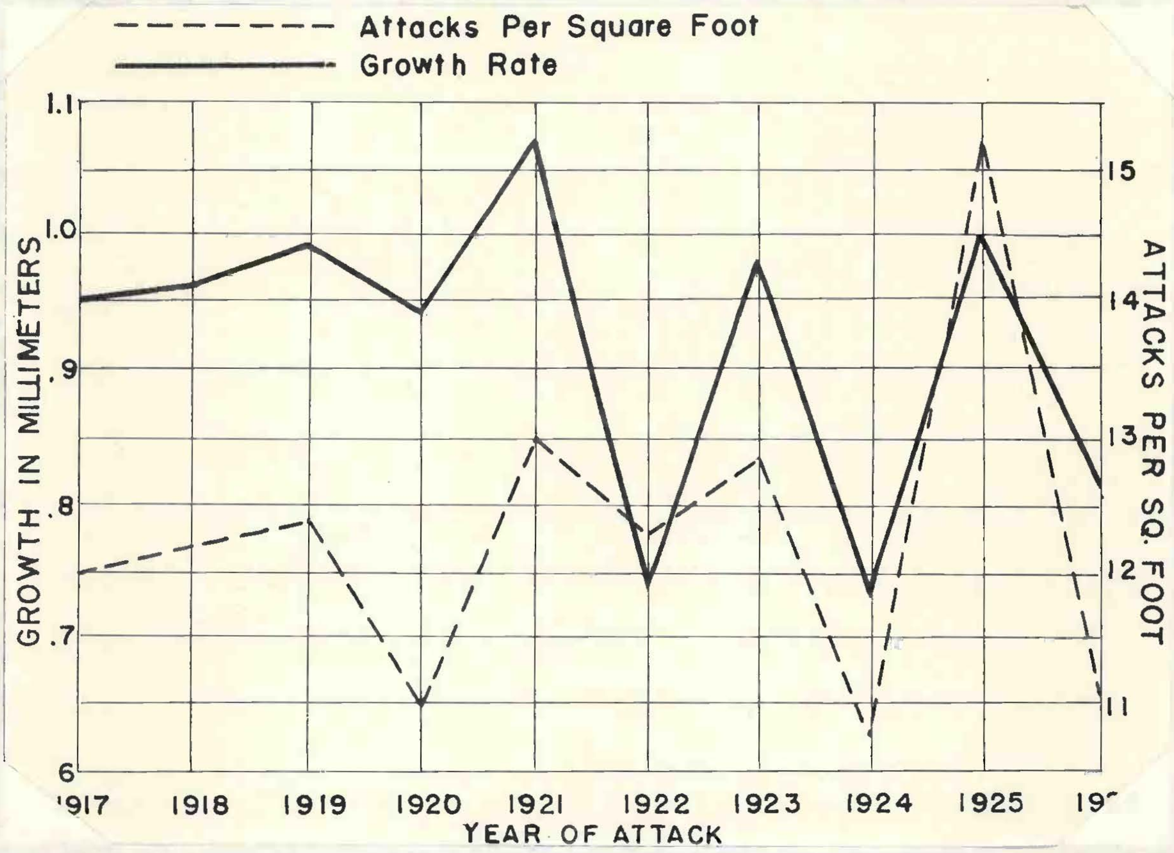


Figure 36.- Number of attacks per square foot of bark surface in relation to average annual growth rate (annually) of ponderosa pine. Jenny Creek Area, Southern Oregon. 1917-1926.

> "The degree of selection exercised by the western pine beetle evidently depends upon the ratio of beetle population to the number of slow-growing susceptible trees.... An increase in the number of such trees tends to increase the infestation, a decrease in the number tends to decrease the infestation. A continued supply of very slow-growing trees usually results in an epidemic such as occurred on the Modoc area. But if after a large (beetle) population has been built up and the number of susceptible trees is reduced, then trees of fairly fast growth will be killed until the beetle population is also reduced by the resistance of the fast-growing trees.
>
> "The highest degree of selection is found when the infestation is at a low endemic stage and fairly static. The degree of selection decreases as an infestation increases and is lowest just after the peak of an epidemic during the first part of the decline in infestation when the beetle population is still high and the number of trees of very slow growth is relatively low."

An illustration of this tendency on the part of the beetles to become less selective during epidemic periods is found in the records of the Cascadel tree selection plot on the Sierra National Forest extending over a twenty-two year period. In 1932 and again in 1942, Struble (U294) analyzed growth conditions on this 80-acre plot and found substantial differences in the growth rate of beetle-killed trees during endemic and epidemic infestations. His conclusions, illustrated by Figure 37, were:

Figure 37 .—Growth rate selection before, during, and after epidemic in percent of total insect-killed trees occurring in each growth rate group for each period.

(Page 341a follows)

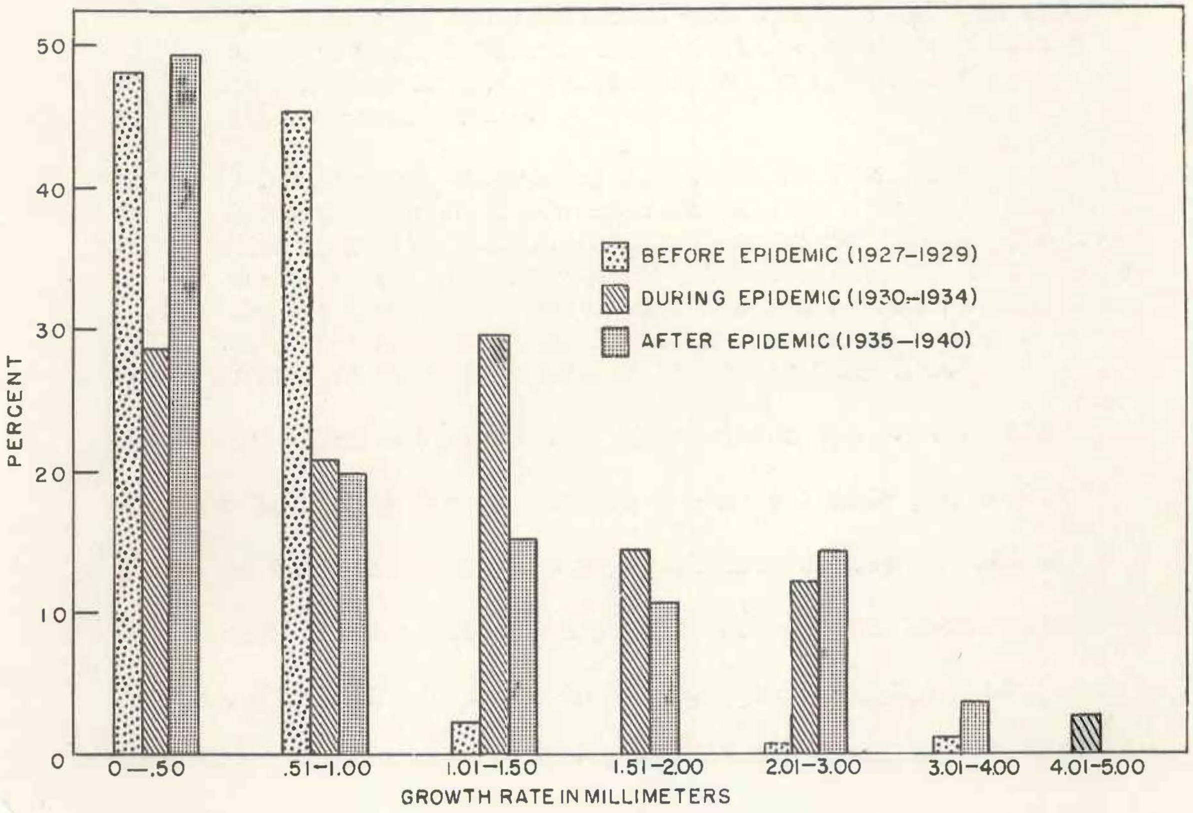


Figure 37.-- Growth rate selection before, during, and after an epidemic, in percent of total insect-killed trees occurring in each growth-rate group for each period.

> "Under endemic conditions on the plot (1918-27), slow-growing trees were selected by the western pine beetle in the greatest percentage of cases; most of those killed were growing less than 1.00 mm. per year in average radial increment for the ten-year period prior to death.
>
> "This preference was diminished during epidemic years (1930-34) when there was a distinct tendency for the beetles to attack faster-growing trees; moderately growing trees (average 1.9 mm.) were selected more often than the slower-growing trees."
>
> "The return of endemic conditions (1935-40) was accompanied also by a gradual return of selection preference for slower-growing trees."

In 1940 Salman made a study on the Modoc National Forest of radial growth in relation to mortality of high risk trees with incipient flathead infestations. His study (U279) took into consideration not only the current rate of growth in high-risk trees, but also the length of the period during which these trees had been in a slow growing condition. Salman's conclusions were:

> "1. The types of trees in which most of the loss has been recorded, i.e. high risk trees, are generally the slower-growing ones.
>
> 2. The slow growth rate is of recent origin and probably temporary, to be terminated either by death or recovery.
>
> 3. Growth abnormalities (missing rings) tend to occur more often in the high-risk trees.
>
> 4. No apparent relation was found between crown characters used in rating risk and any particular type of growth pattern."

In 1940-41 Keen made an analysis of growth conditions from increment cores taken from survey plots in eastern Oregon. He found "that a 15-increment-core sample from 'index trees' (Class 2A or 3A) on a given plot gives a reliable basis upon which to compare relative annual growth differences between plots." (U156). The maximum error of the mean from such a sample was approximately 16 percent. His study (U156) compared the growth rate in beetle-killed trees over a long period prior to death with that in living check trees;and compared the growth in different age and vigor classes of his tree classification. From this study of radial growth measurement from 550 trees, the following conclusions were reached:

> "1.Growth patterns of beetle-killed trees were similar to those of living trees,except that on the average beetle-killed trees were much more complacent in their growth and this characteristic was evident for fifty years or more preceding death.
>
> "2. The growth rate of beetle-killed trees is much slower than the general average of living trees in the stand, and this inferior growth rate has been characteristic of such trees for a long period of time. In this study, beetle-killed trees on the average were found to be growing less than 0.7 mm. per year during the past thirty years. (See Figure 38)

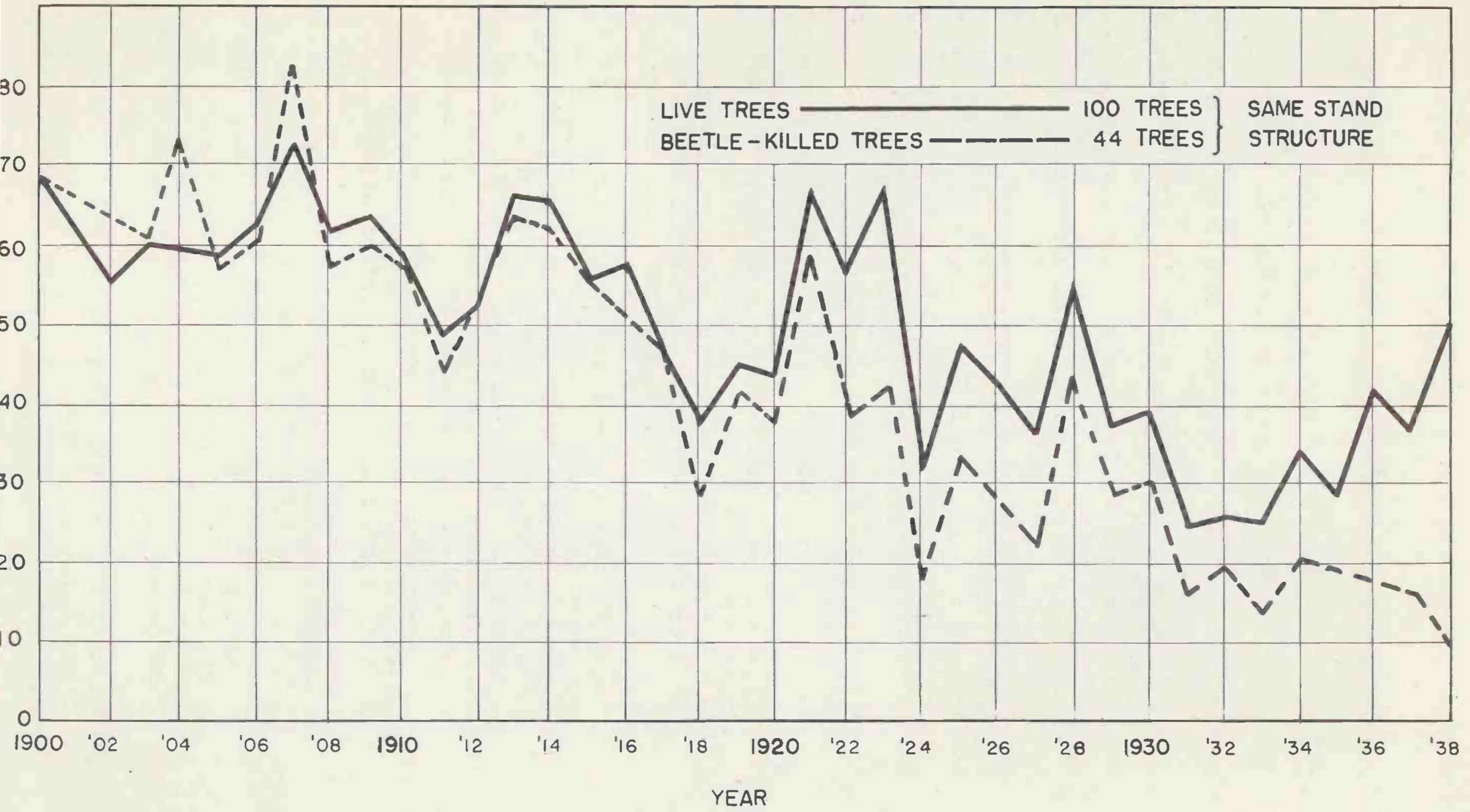
Figure 38 .--Growth comparison between live and beetle-killed trees 1900-1938, Goodlowe Mountain Pl~~a~~ot, Fremont National Forest, Oregon. — ?

> "3.Susceptible tree classes were found to be growing on the average more slowly than the average beetle-killed trees in the decades preceding 1910, while the resistant tree classes were found to be growing at a faster rate. In the decade preceding death,growth of the beetle-killed trees was further reduced to the minimum of any tree class (4C).
>
> "4.Within any tree class, the beetle-killed trees were found to be those growing more slowly than the average of that tree class."

(Page 343a follows)

Figure .-- Growth comparison between live and beetle-killed trees 1900-1938, Goodlow Mountain Plot, Fremont National Forest, Oregon.

— ?



> "5. A general retrogression in growth rate of 1940 beetle-killed trees, more pronounced than in living trees, started in 1917.
>
> "6. Death was preceded by five years of rapid growth decline in opposition to the growth trend of trees that lived.
>
> "7. Except for the change in growth rate, nothing was found in the pattern of beetle-killed trees which would be helpful in differentiating them from other slow-growing trees of susceptible tree classes."

In the general application of the results of this study to practical use in the marking of high-risk trees, Keen commented:

> "There is little hope for using radial growth characteristics for field determinations of high-risk trees or in picking trees which are about to die, by a field examination of increment cores, even though this is a fairly reliable indicator of changes taking place in a tree's vigor and its resistance to insect attack."

It was not until 1942 that Bedard (U16) raised the question of what constitutes a reliable measure of growth vigor. Commenting upon previous studies on the relation of tree growth to resistance and susceptibility to beetle attack, Bedard stated:

> "The radial growth of trees has long been used as a standard measure of tree vigor and its response to various environmental factors. However, the physiological concept of growth in woody plants considers four main meristem regions which produce vertical elongation of the main axis, horizontal expansion through branching, secondary thickening, and leaf development. This places the main meristems in *Pinus* at the shoot tips, near the root tips, at the cambium, and at the base of the needles.

> "As far as could be ascertained, most of the work which has been done with tree growth deals with the activity of a single, or at most two, growing regions. Only one case could be found in which the worker studied all four meristems at the same time. Leader elongation and cambial growth have been most frequently investigated, but only rarely have measurements of both of these activities been recorded simultaneously for the same individual."

By applying different nutrients and water to the soil, Bedard (U22) was able to show differential effects in the various meristems of young pines (see page 408). He concluded that the different soil treatments when compared with untreated trees showed "the inadequacy of any one meristem as an indicator of tree vigor. Needle development, considered as to weight, length and complement, appears to be the best single indicator of vigor."

Conduction.— Studies by forest entomologists on the relation of conduction to susceptibility have largely been incidental to the disturbance of this function caused by the work of organisms and insects associated with the western pine beetle. (see pp. 316).

We find, however, that some studies have been made of conduction in high-risk ponderosa pine by West (U319), Salman with Johnson (U277), and Patterson (U219).

The first of these studies by West was carried out on the Modoc National Forest in 1938 with the primary purpose of determining if the wood of very high risk trees could be preserved prior to attack of the beetles by injecting copper sulphate into the sapstream. The first difficulty that West ran into was ineffective distribution of the chemical because of failure of the conductive system in most of the high-risk trees which he selected for treatment. This was specially true of trees with decadent crowns. Conduction of the chemical was erratic and followed limited channels up through the sapwood layer. Patterson encountered similar conditions in later attempts to introduce preservative chemicals into high-risk trees by the sawkerf method. The results of these experiments add weight to the theory that in high-risk trees the conductive system has deteriorated to such an extent that the tree is unable to resist the attack of the beetle.

The studies of Salman and Johnson (see p.264 Section III) were concerned with the relation of tree susceptibility to the healed-over scars of mines made by flathead larvae in the cambium area. It was demonstrated by special technique that these scars have a definite blocking effect upon the movement of liquids through the wood layers immediately around the scars and are thus detrimental to normal conduction. Since the incidence of flathead infections of high risk trees in eastside pine types is high, they are undoubtedly a factor in the general susceptibility complex. On the other hand it has been shown that successful incipient infestations of the flathead occur mostly in slow-growing trees, so that the conductive function may have been deteriorating at the time of attack.

Transpiration.— In their studies of tree susceptibility, forest entomologists have not made any apparent attempt to distinguish between the functions of conduction and transpiration. These two functions are so closely linked that failure of one will inevitably result in deterioration of the other.

Although no formal reports dealing with transpiration are available, some attention has been given to the effects that follow complete defoliation of the tree. When insects or fire remove the foliage, or the limbs are lopped off, transpiration through the-leaves ceases. This has been found to result in an accumulation of excess moisture in the inner bark and sapwood (see "sour-sap" page 165,Sec. III)which is unfavorable to the development of western pine beetle broods.

Moisture content of the tree.— Beal (U3) made a study in eastern Oregon to determine whether lack of moisture in the phloem tissues of the tree is a contributing factor to susceptibility. He approached the problem by using as a basis the known degree of susceptibility in the different classes of the Keen tree classification. Beal collected phloem samples from representative trees in each class. These samples were distributed so that there were five duplicating samples from each crown class in each age group - making 80 samples in all. Phloem moisture was determined on a dry weight basis. From the correlations which he obtained by plotting phloem moisture content against the susceptibility rating in each class, Beal concluded that:

> "There exists a very close correlation between the phloem moisture content of western yellow pines and their susceptibility to attack by the western pine beetle. Generally speaking the moisture of the phloem decreases with the size of the crown, there being little difference in the age classes. The beetle loss increases as the moisture decreases until a point is reached which appears to be too dry to attract the beetles. This condition is to be found with the (D) crowns."

Hall (U84) repeated this study in August 1948 by sampling the phloem moisture of four trees in each of Keen's 16 tree classes at Black's Mountain Experimental Forest in California. This test failed to show any consistent association between phloem moisture and tree class, or between phloem moisture and risk class.

Records kept on phloem thickness showed a broad association with both tree class and risk. The average phloem thickness for Class A trees was 0.30 inches; Class B. was 0.24 inches; Class C was 0.16 inches, and Class D was 0.13 inches. The average phloem thickness by risk was as follows: Risk I - 0.27 inches; Risk II - 0.20 inches; Risk III - 0.16 inches, and Risk IV - 0.13 inches.

Condition of the root system.-- In the attempt to recognize susceptible trees, forest entomologists have been forced to rely mainly on visible characters of the crown and other parts of the tree which are found above ground. It has been recognized, however, that this affords only a partial picture of the tree's condition. Equally important to tree vigor and its capacity to resist beetle attack is the root system, which can only be examined and studied after the soil has been removed. For large mature trees which compose most of the high risk in pine stands, this is a laborious and highly expensive job. The cost factor undoubtedly accounts for the fact that the only studies of root systems have been limited to a few cases where favorable conditions were found for exposure of the roots.

In 1926, Person (U229) partially pruned the roots of two fast-growing ponderosa pines to see if reduction of the root area would result in such trees becoming attractive to the western pine beetle. Although these root-pruned trees did attract some Dendroctonus valens attacks, Person considered the results as negative and concluded that: "Root-pruned trees are evidently not attractive (to the western pine beetle) at least during the first season following treatment."

Since this experiment was concerned with artificial injury to the roots of normally vigorous trees, it did not shed much light upon the natural deterioration of the root system in high-risk trees.

. This exploratory attempt by Person was not followed by further root studies until 1939 when West (U320) examined and studied the root systems of five ponderosa pines with known risk characteristics which had been upturned by windstorms. The next year J.W. Johnson (U107) examined parts of the root systems of six ponderosa pines by excavating with hand tools. In 1941 Bedard (U14, U15) used hydraulic pressure to wash the root systems of six ponderosa pines with known risk ratings. Thus up to the present time all that is known about the relationship between condition of the root system and susceptibility to bark-beetle attack is based upon twelve standing trees and five windfalls.

West's study of the exposed roots of windthrown trees was made in eastside pine type on the Modoc National Forest. The material included one low risk and four high trees; he found that the low-risk tree and three of the high-risk trees had extensive and apparently healthy root systems, but the fourth high-risk tree had a root system which was much reduced and abnormal.

J.W. Johnson's six trees were in the same Modoc areas as West's. During the early summer of 1940 he used CCC labor with pick and shovel to remove the soil from selected roots of five low risk and one high risk ponderosa pine. The crowns of these six trees were also carefully studied and an inventory taken of the Matsucoccus scale population on limbs and twigs and the incipient flathead infestation on the main bole. The following summary is found in Johnson's report:

> "The root systems of six trees were partially uncovered and their condition noted during May and June,1941. Five of these trees were Risk I and one was Risk IV. The root system of the Risk IV tree showed many more dead large roots and branches, and was considered to be in poorer condition than the root systems of the Risk I trees."

Bedard's study of the root conditions of susceptible trees was initiated by a review of the literature pertaining to root anatomy, morphology, and physiology. His conclusions based on this review were:

> . "Root form is quite specific and in addition there is considerable reciprocity between the crown and root system. Root development is of critical importance to continued plant growth. It is important that root development keep pace with crown development."

This review also included a summary of the two previous studies on ponderosa pine root systems in the Modoc area and Bedard's first report (U14) outlined a field study which was carried out in the Klamath Basin during the summer of 1941. He selected three high-risk and three low-risk mature ponderosa pines in pairs on a site where it was practical to wash out the root systems with water. The results did little more than reveal some physical differences between high- and low-risk trees.

> "In the low risk trees, the roots branch from the main axis deeper below the soil surface and penetrate the soil at a greater angle than the roots of high-risk trees. Additional slight differences were found but they were not statistically significant. These differences were that high risk trees had fewer roots of smaller size, a greater percentage of dead roots, and fewer small feeding roots per lineal foot."

In summing up these preliminary studies, Bedard listed the following factors as essential to root development - physical and chemical properties of the soil, soil moisture, mycorrhizae, soil gases, heat, toxic decomposition residues, competition, beneficial plant associates, and heredity. Most of these were considered in a further study of root conditions in very small trees and potted seedlings by a long series of soil treatments. This work was reported upon in 1944 (U22) and will be reviewed under edaphic factors.

None of the root studies to date have brought out any significant relation between condition of the mycorrhiza on the roots and the susceptibility of ponderosa pines. Difficulties in the way of thorough examinations of the root systems of any number of trees have apparently discouraged even preliminary explorations in this field.

Pathological Factors

In many cases fungi, disease, and other pathological agents affecting trees definitely contribute to increasing their susceptibility to insect attack. Frequently insects are the vectors of plant diseases or there may be a symbiotic relation between the disease and insect which works to the advantage of both. Some study has been given to pathological factors affecting ponderosa pine and their relation to increasing this tree's susceptibility to western pine beetle attack.

Fungi.--

Needle fungi.-- The common Lophodermium fungi which is associated with the early shedding of the older needle fascicles may at times produce a color appearance of pine foliage which resembles the fading color phase. When these attacked needles drop, the tree takes on a thin-crowned appearance for a season or two until it builds back its normal needle complement. However, no studies have been made which indicate that the effect of these fungi upon the tree produce permanent deterioration of the crown. Apparently they do nothing more than to accelerate at times the normal shedding of the older needles. The earlier opinion of the pathogenicity of Lophodermium has been discounted by later studies and Dr. Willis Wagener in a note on the subject states: "It seems safe to say that the fungus has no appreciable effect on the growth of ponderosa pines or on their risk rating."

A needle-cast fungus, identified by Dr. Willis W. Wagener as *Hypodermella medusa* caused some confusion in risk ratings on the Black's Mountain Experimental Forest during 1940. This fungus usually attacks only the older needles, those two or more years old. In 1940 it attacked certain trees which had previously been classified as low risk and by causing the shedding of practically all needles except those of the 1939 and 1940 growth, resulted in a more sever~~al~~e appraisal of risk than would otherwise have been given. This situation was complicated by a drought which caused shortened needle growth in 1939 and preconditioned some trees to an increase in the needle disease. The condition noted was only temporary and normal conditions of needle growth were restored in subsequent years.

Subsequent examinations by Dr. Wagener at about two year intervals from 1940 to 1951 showed that the same trees always were affected with the disease, but that the 1940 infection was heavier than that in any of the subsequent years. Increment borings showed a progressive decline in growth rate for the affected trees, and hence an increase in bark beetle susceptibility.

Elytroderma _deformans_ is a serious needle disease of ponderosa pine throughout this tree's range in the West. It also attacks Jeffrey pine, lodgepole and pinon pine in the Western States and several species of pine in the East. Severe damage, however, has been reported only on ponderosa and Jeffrey pine in California, Oregon, Washington, and Idaho. Recently it has become exceedingly destructive to certain ponderosa pine stands in central Oregon and southern Idaho. These outbreaks have been under study by the Division of Forest Pathology and a manuscript by Dr. P.C. Lightle, covering the most recent information concerning it, is in course of publication. 13/

The fungus has a life cycle of one year. It attacks needles of the current year's growth during the latter part of the growing season. By the next May and June the needles turn a reddish color, for most of their length, while the base remains green; or the entire needle may discolor. Apparently the fungus causes some toxin which is carried down into the stems and causes internal lesions of the twigs. Repeated attacks cause dwarfing of the twigs, the formation of loose witches' brooms, or death of the twigs and branches. Trees heavily affected year after year become weakened and ultimately succumb to the disease or to the attack by bark beetles.

13/ Lightle, P.C. The pathology of _Elytroderma_ _deformans_ on ponderosa pine. Phytopathology 44(10):557-569, 1954.

While the disease has been known since 1913, and periodically has appeared in spot infections, it was not until about 1945, when it killed out nearly the entire ponderosa pine stand on the Johnson Creek area of the Ochoco National Forest in Oregon, that its potential destructiveness was fully appreciated. Since then it has persisted in epidemic form in a number of areas in eastern Oregon and on the Boise and Payette National Forests of southern Idaho. The disease seems to favor cool ravines or basins, particularly at the higher elevations for pine where it is associated with fir, lodgepole, or larch.

The effect of this needle disease in weakening pines and causing them to become more susceptible to bark beetles has been of great concern to foresters and has been watched by forest entomologists with much interest. On the Ochoco National Forest, the Johnson Creek infection developed so rapidly and with such virulence that trees were quickly defoliated and killed by the disease. The phloem and sapwood of these defoliated trees developed excessive moisture or a "sour sap" condition, which apparently made them unattractive to D. brevicomis. No bark beetle outbreak developed in these disease stricken areas. In the southern Idaho forests, the disease progressed more slowly. Trees were repeatedly attacked, progressively lost foliage, developed twig lesions, and decreased in growth rate. This decline in tree vigor increased their susceptibility to bark beetles. As a consequence, there has been a general widespread increase in beetle activity in the disease infected areas. On the Deadwood Reservoir area of the Boise National Forest, a western pine beetle outbreak developed such intensity in the needle disease weakened timber that a control project had to be initiated. In 1951, 2200 trees were treated on this project. In 1952, 900 trees were treated which reduced the infestation to 200 trees. The area was subsequently logged in 1953.

On the Warm Lake area of the Payette National Forest and on other areas in southern Idaho and eastern Oregon, the deterioration of the trees' crown vigor caused by progressive infections of this needle disease has created a serious problem of risk rating and marking for selective cutting. Due to progress of the disease, some areas have had to be remarked and relogged several times until the infected areas were practically clear cut.

Root fungi.— A root disease of young Jeffrey pines was first noted in 1934 on the Lassen National Forest in northeastern California by K.A. Salman and studied by A.J. Olson (95), who named it as a new species. In 1941, DeLeon found a root disease to be contributing to the dying of many Jeffrey pines on the Mount Laguna Recreational Area of the Cleveland National Forest in southern California where a bark beetle control project was in progress. This disease was studied by Dr. Willis Wagener who determined it to be Fomes annosus. Later it was shown that this was the same disease as described by Olson. A series of field studies was then started by Dr. Wagener to determine the prevalence and distribution of this fungus on the root systems of ponderosa and Jeffrey pines. In a letter to the Regional Forester dated October 16, 1946, Wagener reported as follows:

> "Within the past few weeks explorations around the bases of distressed, dying or recently dead trees in parts of northern California have shown that root killing of large pines by *Fomes annosus* is not confined to southern California, but occurs in at least some portions of northern California as well. Part of the field examinations were made jointly with Dr. Donald DeLeon of the Berkeley Laboratory and part by our office alone. The disease has been found in portions of the eastern Plumas, Lassen and Shasta National Forests, including the Black's Mountain Experimental Forest, and in Lassen Volanic National Park. In addition to ponderosa and Jeffrey pines, sugar pine has been found to be affected and there is some indication that white and red firs are subject to attack."

Additional studies by Wagener and Cave of this disease uncovered much new information concerning its behavior and relation to bark beetle attack. In their published article (129) they state:

> "Killing of the bark and cambium of attacked trees by the fungus (*Fomes annosus*) ordinarily extends little above the ground line. Except in quite small trees, the balance of the trunk is usually invaded by bark or wood boring beetles before fading of the foliage occurs as a result of girdling from the fungus attack, and thereafter the tree appears superficially no different from one killed primarily by bark beetles.
>
> "Bark killed by the fungus separates readily from the wood. The separated surfaces are usually a characteristic light brownish buff in color, finely penciled with light russet, or the reverse. A thin weft of whitish mycelium is also usually visible between wood and bark.... Another confirmatory feature in the cambial region and in bark killed by the fungus is the absence of galleries of the red turpentine beetle (*Dendroctonus valens* Lec.). This beetle and its larvae are usually active in the basal portion of pines killed primarily by insects but apparently avoid bark invaded by *Fomes annosus*. Roots initially attacked by the fungus become heavily infiltrated with resin. After a tree is killed the fungus remains active as a wood-rotting organism in the roots and butt.

> "The disease spreads from an initial center, usually a stump or snag, to surrounding trees through contact of overlapping root systems, forming a roughly circular opening in stands on level ground.
>
> "In addition to the direct threat to surrounding trees offered by the fungus, an accompanying danger has been observed in one or two localities near the lower ecological limits for pine. Here bark beetles, presumably species of *Ips*, have developed in trees killed primarily by the fungus and, on emergence, have extended their attack to adjoining trees showing no evidence of the disease at the base. In other infected districts less marginal for pine no similar extension of bark beetle attacks from diseased trees has been noted, but it is quite possible that such trees may contribute to the building up of bark beetle epidemics by providing a favorable environment for the maintenance of a small beetle population during periods when infestation is in an endemic status." 14/

Another root disease reported by Bongberg on the Black's Mountain Experimental Forest in a memorandum dated March 28,1939 was determined by Dr. W. Wagener as a species of *Leptographium.* The tree apparently had been killed by this fungus which originated in the roots and invaded the main bole above the root collar, and caused a brown stain in the sapwood. The only insects found in this fading tree were incipient larval mines of *Melanophila gentilis* and adults of *Hylurgops subcostulatus* near the base, both of which were considered to be secondary.

14/ In reviewing the above paragraphs, Dr. Wagener commented in 1954: "At the time this article was written, we were not aware of the fairly long-period rise and decline in incidence which evidently is tied in with soil moisture in some way, though we are not certain what the particular conditions are that favor the disease. For the last few years it has been at a rather low ebb in most of California."

The common oak root fungus *Armillaria mellea* has frequently been observed killing ponderosa pines of small diameter, usually trees in intermediate or suppressed positions and of poor vigor. Usually these trees are attacked in the main bole by *Dendroctonus monticolae*, *Ips emarginatus*, or flatheads. The infrequency of trees found killed with this fungus would indicate that it is not a very important primary root disease in ponderosa pine stands. In portions of the pine stand where oaks exist, the fungus often develops on decadent oak roots and extends from these to adjacent pine roots.

Heart rots.—— Observations indicate that there may be a fairly high degree of correlation between heart rots in ponderosa pine and high risk to bark beetle attack. Heart rots are common in old trees of poor thrift, in spike-top trees, and those with broken tops and limbs. Since these decadent trees are often of high risk, it is understandable why there should be some degree of positive correlation with heart rots. Also, it may be that heart rots actually cause a decline in tree vigor and thus contribute to susceptibility. This relationship in ponderosa pine has not been given any careful study.

Dwarf mistletoe.— Quite early in western pine beetle investigations, the idea was suggested that dwarf mistletoe, *Arceuthobium campylopodum* forma *typicum* (Engelm.) Gill and the witches brooms which they produce may cause ponderosa pines to become susceptible to western pine beetle attack and thus serve as focal points for infestations. (134) Observations have been made on this point for many years without conclusive evidence having been developed.

During the field seasons of 1914, 1915, and 1916 H.E. Burke (15) spent part of his time at Pyramid Ranger Station above Placerville, California on a project "The relation of mistletoe on living trees to attacks by tree-killing insects." He "found that 64 percent of virgin growth yellow pine...in typical areas near Pyramid were mistletoe infected. The conclusions drawn from the study were (a) trees infected by mistletoe are not more subject to attack by *Dendroctonus* beetles than trees not so infected, in fact it looked as though badly infected trees were less liable to attack than trees free of infection; (b) trees weakened by mistletoe do not contribute to the increase of *Dendroctonus* beetles."

Keen (U122) in comparing the distribution of 372 trees killed by western pine beetle on the Lamb's Mine Unit at Ashland, Oregon, found that 57 percent were infected with witches broom and 38 percent with mistletoe, but did not determine what percent of the green stand was similarly affected. Hopping (51) summarized the information on the occurrence of mistletoe infection on 1,656 trees treated on the Susan River Control Project in the eastern Lassen. This record showed that mistletoe was present on from 15 to 26 percent of the infested trees, but Hopping also failed to determine what percent of mistletoe infected trees occurred in the green stand so that the degree of selection was not shown.

Out of 6535 tagged trees on 30 10-acre plots established in eastern Oregon in 1938 and 1939, the number killed by beetles in 10 years out of those rated with mistletoe or witches broom were as follows:

	Number Killed	Out of Total	Percent Killed	Mortality Ratio
1.Small amount of mistletoe	0	25	0	0
2.Large amount of mistletoe	3	19	15.8%	3.6
3.Small witches brooms	12	171	7.0	1.6
4.Large witches brooms	22	102	21.6	5.0
Average of total stand	286	6535	4.37	1.0

These data confirm the suspicion that mistletoe infected trees are more susceptible to beetle attack than normal trees. Trees with large amounts of mistletoe are 3.6 times as susceptible, while those with large witches brooms are 5 times as susceptible. This gross relationship does not take into account the fact that trees heavily infected with mistletoe are probably also the older, more decadent tree classes in the stand.

Insect Injuries

The extent to which other insects may contribute to the weakening and increased susceptibility of ponderosa pines has been covered under "associated insects" in Section III ,pp.235- 273

In the case of Melanophila californica, it was shown that the scars of incipient larval mines cause a blocking effect upon conduction in the outer rings of the sapwood and thus interfere with normal functions of tree growth. While these scars may inhibit growth to a limited extent, it was also found that slow growth is a prerequisite to attack by flatheads. Salman (U279) found that "incipient infestations tended to occur more often in the trees which died than they did in the stand as a whole."

McKenzie's study (U166) of the scale *Matsucoccus bisetosus* was pointed primarily to determine whether certain phases of deterioration in the crown could be attributed to infestations of this insect. He found no significant differences in scale populations, as measured by number of scales per square inch of bark on stems in comparing high-risk and low-risk trees. However, a special type of injury caused by the scale, i.e. heavy resining in the axils of lateral twigs, was found to be more prevalent on high-risk than on low-risk trees.

The role of defoliators, *Dendroctonus valens*, *Ips* beetles, and the resin midge in rendering trees attractive or susceptible has been discussed in the paragraphs under associated insects in Section III

Mechanical Injuries

Trees injured by lightning, fires, top-killing, girdling or mechanical bark injuries frequently become victims of western pine beetle attack. The degree of susceptibility developed by such injuries has been the subject of numerous studies.

Lightning-struck trees.— Lightning injury was one of the first factors considered to be a cause of the attraction of bark beetles to pine trees. Hopkins (43) states that:

> "In certain sections of the country where a great many pine and spruce trees are struck by lightning during the summer months, these trees furnish exceptionally favorable conditions for the perpetuation and multiplication of pine and spruce beetle.... This is especially true in the southern states where a pine tree struck by lightning attracts the beetles to the spot and they enter not only the injured tree, but attack and kill a number of those surrounding it."

In western pine beetle areas, lightning-struck trees have always been regarded as especially attractive. Hopping (51) states:

> "If there is an epidemic infestation within the area, every lightning-struck tree becomes infested. If, however, the infestation is very slight on an area, lightning-struck trees often escape being attacked."

Keen (61) makes this generalization:

> "Lightning-struck trees appear to be very attractive to bark beetles and very few escape death if beetles are present in any numbers. In fact, unless lightning-struck trees are completely shattered, they rarely die unless attacked by insects."

Although the impression has prevailed that lightning-struck trees are attractive to bark beetles, there are no studies on record which show the degree of preference or percent of lightning-struck trees that are attacked by beetles. Since it has not been shown that the ordinary longitudinal scars made by lightning down the main trunk affect the growth rate to any extent, there is no explanation for the attraction unless it is due to changes which take place in the sapwood and phloem tissues as a result of the electrical charge breaking down the cells.

Fire scars.-- Basal scars or "cat-faces" made by fire also result in exposure and overheating of the cambium and sapwood. The results arrived at in the Northfork Burn study by Miller (U197) and on the Sugar Hill fire by Salman and Wohletz (U252) indicate that the common basal fire scars in pine stands and the subsequent extension of such scars by repeated fires has no effect upon the susceptibility of the trees to bark beetle attack.

On the other hand, Bedard (U13) in analyzing the characters associated with high risk found that "fire scars were more abundant on high risk trees than on normal trees" and suggested that they should"not be overlooked as a possible clue to the cause of (some) tree decline."

On the risk plots of eastern Oregon, Keen found that trees with small fire scars (less than 50 percent of the basal circumference) were not particularly susceptible, but that those with large fire scars were susceptible. Out of 233 trees so classified, 17 were killed by beetles in 10 years or 7.3 percent. Since the average percent of trees killed in the stand was 4.37 percent, these large fire-scarred trees showed a mortality ratio of 1.7. In other words, they were killed nearly one and three quarter times as frequently as the average tree in the stand.

Top-killing.— Keen (U122) found on the Ashland areas that trees recently top-killed by Ips, or top-killed and abandoned, were definitely more attractive to D. brevicomis than uninjured trees. Over 26 percent of such trees were attacked by D.b. in one season. On the Cascadel area, Person (U229) found that 43 percent of trees topkilled by Ips confusus were attacked by D. brevicomis within two years after topkilling.

In the 1938 survey report for the Modoc National Forest, R.C. Hall reported that old top-kills were an important factor in the seasonal loss:

> "Of the total volume loss for 1938, previously top-killed trees made up 36 percent of the volume. However, the indirect effect of top-kills in the 1938 loss appears to be of additional importance, because in a large percent of cases, old top-killed trees served as a focal point of infestation in a group, where the insects first attacked the top-kill and then overflowed into adjacent vigorous trees."

J.W. Johnson (U109) analyzed the distribution of top-killed trees in the 1940 loss on Black's Mountain Experimental Forest. Of 621 beetle-killed trees found that year, 33 percent of the trees and 38 percent of the volume had been previously top-killed. In the green stand as a whole, only 6.7 percent of the trees and 9 percent of the volume was in the top-killed category. Johnson concluded that:

> "Top-killed trees show a death rate almost five times the expectancy based upon their occurrence in the green stand. This mortality rate is seven times that of trees without top-kills.
>
> "All top-killed trees except the young dominants appear to be markedly susceptible to insect attack. Top-killed trees of mature and overmature age appear to be particularly susceptible to insect attack."

On the Oregon risk plots, the relative susceptibility of active spike tops, old spike tops and broken top trees was shown as follows:

Tree condition	Trees Killed	Out of Total	Percent Killed	Mortality Ratio
Active spike top	29	85	34.1	7.8
Old spike (not active)	37	408	9.1	2.1
Broken top (not active)	5	38	13.2	3.0
Total stand	286	6535	4.4	1.0

This record shows that active spike tops are very susceptible, while old spikes are taken twice as frequently as the average tree and broken tops are taken three times as often.

Freezing.-- Salman (U273) observed that the low winter temperatures of January 1937 on the Modoc National Forest, California, not only killed a relatively high proportion of western pine beetle broods but scorched foliage at the tops of trees and injured the phloem of some trees to such an extent that they were attacked and killed by secondary bark borers. In trees injured by the cold, the roundheaded borers Acanthocinus spectabilis and A. obliquus were, in many cases, the first species to enter the cambium area and were successful in rearing broods. They successfully competed with the flatheaded borer Melanophila gentilis and were assisted by Orthotomicus ornatus and Ips oregoni. The base of these cold-injured trees filled in with Dendroctonus valens, and in some cases this beetle took precedence in its attack over all other species.

Injury to tops of trees from freezing has been reported by Wagener (see p. 267) and may precede attacks by Ips, Pityophthorus and other primary or secondary bark beetles and borers. This type of injury may be a great deal more common than has been recognized, and may be the primary cause of top-killing which has frequently been ascribed to bark beetles.

Other types of injury, girdling, scarring, etc.— Other types of injury and special conditions which make trees attractive to the western pine beetle are described under "Attraction," page 102 - 112 ,Section II

Silvical Factors

The studies just described have all pointed to the slowing down of tree growth as the dominant factor which either attracts the beetles or makes the tree susceptible to their attack. Regardless of whether suppression of growth was induced by environmental conditions, drought, fire injury, defoliation, top-killing, or the inevitable slowing down of growth due to advancing age, the end result was much the same - increased susceptibility to bark beetle attack. But suppressed growth did not provide a complete answer in all cases, for many slow growing trees could be found which survived for years without being subjected to attack.

In addition to rate of growth, the silvical factors of tree age, size, degree of maturity, crown size, position or degree of dominance,and general tree vigor and health were early recognized as being related to growth rate and having a possible connection with tree resistance and susceptibility.

Hopkins (43) noted that the western pine beetle preferred to attack "weakened and felled trees" and "large mature timber" while finding areas of "vigorous, recently mature, or young growth" unfavorable for attack. He did not infer that growth rate was an important element of tree resistance and susceptibility and went to some pains to point out that this beetle attacked healthy trees.

In analyzing the type of tree most attractive to western pine beetle attack on the Lamb's Mine unit at Ashland, Oregon, Keen (U122) found that out of 401 trees killed by western pine beetle between 1914 and 1916, 45.4 percent were "thrifty" trees (by which was meant "young trees before maturity of growth, but not necessarily vigorous or rapidly growing trees"), 35.9 percent were mature trees (by which was meant "trees which have reached their maximum growth and have developed flat crowns"), and 11.5 percent were decadent trees (by which was meant "trees which are old, not vigorous, and in a retarded state of growth"), 7.2 percent were felled trees. But no comparison was made to show how these percentages compared with the distribution of these classes in the stand as a whole.

Tree age or maturity.-- Hopkins (43) stated:

> "Practically all of the more destructive species (Dendroctonus) show a decided preference for the larger and best matured trees and as a rule these are killed first, and the younger timber is not attacked until later, if at all. This is particularly true of... the western pine beetle, and the mountain pine beetle of the West."

While the impression that overmaturity is the most important factor in susceptibility still persists, later studies have shown that it is relatively of less importance than tree health and vigor.

Keen (U148) in comparing the age groups of 27,465 ~~beetle-killed~~ ponderosa pines beetle killed during the four year period 1928 to 1931, as contrasted with age distribution of 22,428 green trees on 16,000 acres of sample plots in southern Oregon and northern California found the following ratio of mortality by age groups.

Note time when data were taken.

Relative Susceptibility by Age

Age Groups	Tree Ages	Apportionment in Trees Total Stand Percent	Beetles Killed Percent	Ratio of Mortality to Stand
1	75 minus	17.6	8.3	.46
2	75-150	25.8	28.2	1.15
3	150-300	29.6	32.3	1.05
4	300 plus	27.0	31.2	1.16

In referring to the above table, he noted:

> "There is very little difference in relative susceptibility by ages in trees over 75 years of age. As has been frequently noted, trees of the bull pine type (age group 1) which rarely exceed 16 inches in diameter in Oregon's site 4, are very resistant to bark beetle attack."

Additional evidence accumulated from surveys in eastern Oregon, Washington, and northern California between 1938 and 1940 with a total sample of 51,409 beetle-killed trees (70) gave the following results:

Age Group	Tree Ages	Apportionment in Trees Total Stand Percent	Beetles Killed Percent	Ratio of Mortality to Stand
1	75 minus	17.7	5.8	.33
2	75-150	25.4	21.4	.84
3	150-300	42.4	42.8	1.01
4	300 plus	14.5	30.0	2.07

This evidence indicates a marked increase of susceptibility in overmature trees and a strong resistance of the young and immature groups.

Bongberg (U31) compared the occurrence of 484,635 board feet of insect-caused loss in pomderosa pine on the Black's Mountain Experimental Forest between 1936 and 1940 and found the highest percentage of volume loss occurring in the overmature age class. He states: "It is evident that risk does increase with age, but age does not become an important factor until overmaturity is reached...Age does not overshadow or outweigh the importance of risk characters as an indicator of susceptibility." This appears to sum up the conclusions reached on the importance of age in the studies conducted so far.

Tree size - selection by diameter.— One of the first selective tendencies recognized by observers was that trees in the middle range of diameters were killed more frequently by the western pine beetle than trees of smaller and larger diameters. This preference could very easily be demonstrated by comparing the curve of diameter distribution for beetle-killed trees with a similar curve for the entire stand. Such a comparison was made by Person (104, U229) using the records from 5,000 beetle-killed trees on the San Joaquin Control Project and the diameter distribution of ponderosa pine in the stand as determined by Burnett Sanford of the Forest Service. These data were all from westside Sierra pine type and showed that:

> "The number of trees killed in the diameter classes between 20 and 30 inches is much greater than proportionate to the number of such trees in the total stand. Evidently the western pine beetle prefers trees between 20 and 30 inches in diameter."

Keen (U148) in summarizing data from six years of sample plot cruising in southern Oregon and northern California from 1927 through 1932, compared the frequency distribution of 49,701 beetle-killed trees with that of 64,159 green trees on these plots by two-inch diameter classes. (Figure 39). This showed a marked preference for trees between 20 and 32 inches d.b.h. which was a confirmation of earlier work.

Figure 39 .— Distribution of green and beetle-killed trees by diameter classes. East-side type. Southern Oregon-Northern California. 1927-1932.

Page 374a follows

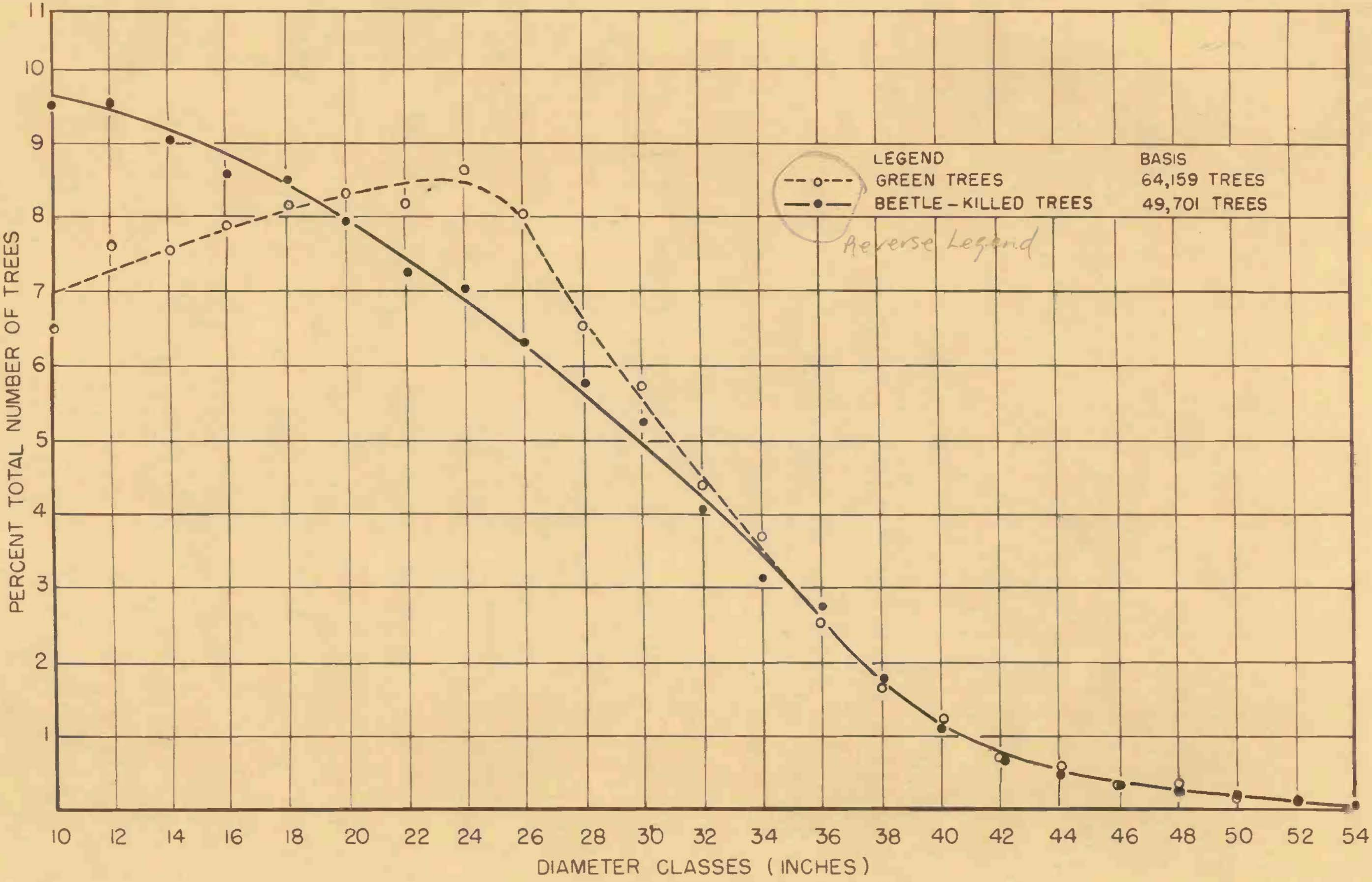


Figure 39.--Distribution of green and beetle-killed trees by diameter classes. East-side type.

Since we cannot attribute to the beetles the faculty to distinguish trees by diameter measurements, why should they select trees within these particular diameter limits? The evidence suggests that the reason is because the greatest struggle of mature trees for dominance is occurring in this diameter range. Young trees up to 20 inches d.b.h. do not suffer too much from competition. Then, as maturity approaches, the struggle becomes intense and many stems have to be eliminated. After the trees reach 32 inches d.b.h. the bulk of the trees in the stand are made up of mature and overmature dominants that have survived the struggle and are well fitted to maintain their place of dominance unchallenged.

Crown size, position or dominance.— Person in his studies of tree selection by the western pine beetle (U228) considered crown class, size, and shape in relation to susceptibility. About 200 ponderosa pines killed by the western pine beetle were marked on the Cascadel area in 1925 and classified as to dominance, crown shape, length, and width. However, he did not have a similar comparison for the green trees in the stand and hence could not draw any conclusions as to degree of selectivity. He stated, however:

> "It is evident that the average tree of dominant and co-dominant crown class with rounded top and medium length and width of crown suffers the heaviest loss. It is surprising that the number of intermediate and suppressed trees killed is so small. This is probably due to the fact that the total number of such trees in the stand is small because of the openness of the stand."

Dunning (31) in setting up his tree classification brought out the fact that "the small crowned mature co-dominants of class 4 are indicated to be the most liable to insect damage."

In a later report on his Cascadel studies (U233),Person stated his conclusion as to the relation of crown form to susceptibility as follows:

> "The susceptibility of a tree varies inversely with the size of its crown. Trees with long, wide crowns are least susceptible to attack by the western pine beetle and trees with short, narrow crowns are most susceptible."

Keen (U148) in his study of relative susceptibility of ponderosa pine to bark beetle attack compared the frequency of attack in four crown vigor groups which to a large extent represented four degrees of vigor, crown size, and dominance. The results from comparing a sample of 49,701 beetle-killed trees with 64,159 green trees on sample plots in southern Oregon gave the following results:

Relative Susceptibility by Crown Classes

Crown Vigor Group	Vigor	Apportionment in Trees Total Stand Percent	Beetles Killed Percent	Ratio of Mortality to Stand
A	Full vigor	36.0	12.0	.33
B	Moderate vigor	36.0	35.3	.98
C	Poor vigor	21.2	43.4	2.05
D	Very poor vigor	6.8	9.3	1.37

Keen states:

> "It is evident from these comparisons that crown vigor is much more important in determining susceptibility than merely age. In other words, the fact that a tree is old does not necessarily make it a poor risk, while the character of its crown and its position in the stand are much more important considerations."

Additional study of these factors were conducted in connection with studies of tree classification and will be discussed under that heading.

Crown vigor and health.-- Crown vigor or thrift was also recognized by Hopkins as an important factor in the selection of trees by the western pine beetle. He states (43): "While it appears that this species prefers to attack weakened and felled trees, or isolated healthy ones, it often attacks large numbers of healthy trees and causes extensive depredations."

The attraction studies started in 1916 (see ~~Part~~ page 102) also indicated this beetle's preference for felled, top-killed trees and those of slow growth. Many other studies have followed, all of which were directed towards finding symptoms of poor health, weakness or injury which would give a clue to the problem of susceptibility. As most of this work was done in connection with the development of tree classifications, it is discussed under this heading.

Key trees in groups.— In contradiction to the suppressed growth explanation is the fact that under epidemic conditions the western pine beetle attacks large groups of trees which include trees in all conditions of crown and growth vigor. However, in each of these groups it is usually possible to find a tree to which the beetles are at first attracted and on which they concentrated during the first phase of the group attack. This initial "key" tree as a rule exhibits one or several of the symptoms of susceptibility, such as suppressed growth, deteriorated crown, or some special injury to the trunk, crown, or roots, such as top-kill, lightning, or recent wind or snow break. Once the beetles have occupied the bark area of this key tree, more beetles coming to the vicinity attack adjacent trees, regardless of their condition, until the beetle population coming to that particular center of attraction has been absorbed (see "Attack," pages 37-46, Section II).

These susceptible key trees are undoubtedly quite important to the ecology of the western pine beetle. Under endemic conditions most of the trees that are attacked are key trees which the beetle selects in ponderosa pine stands that are generally resistant to attack. In this way the western pine beetle is able to perpetuate its population by breeding in weakened trees when the general stand conditions are unfavorable to an increase of its numbers.

Tree Classifications

Classification of trees according to age and vigor as indicated by the size, form, and condition of the crown, and certain characteristics of the bark, has been a further step in the recognition of susceptible trees. These classifications are all based on visual characters which can be readily seen and appraised in the woods. At least three such classification systems have been developed which have silvicultural as well as entomological uses and are adaptable to ponderosa pine stands where western pine beetle infestations are prevalent.

Dunning tree classes.— Dunning (31) was the first to set up a tree classification for ponderosa pines in the uneven-aged [selective] forests of the Sierra Nevada Mountains by defining seven classes which could be distinguished mainly by age characters and form of the crown. The classes were intended as a measure of tree vigor to serve silvicultural purposes, such as the selection of trees for cutting on timber sales. The fact that Dunning's classes with least vigor, mainly Classes 7, 4, and 5, were found to be suffering the highest mortality from beetle attack opened up an entomological application for this classification.

Keen (U140) applied Dunning's classes to 13,160 beetle-killed ponderosa pines and a sample of 10,053 green trees in the 1927 survey of forty-seven 640-acre sample plots in eastern Oregon, totalling 19,680 acres. This study confirmed Dunning's findings in showing the greatest preference for Classes 7, 4, and 5, all of which were making annual growth of less than 1 percent of the basal area. Keen also concluded that:

> "Eighty percent of the loss by volume consists of the overmature dominant trees of Class 5...In dominant classes, the average volume of trees killed by beetles is much lower than the average volume of the class as a whole... On good sites there is a marked selection of the suppressed and co-dominant trees of Classes 4 and 7. As the site becomes poorer the proportion of loss increases in the dominant classes 1, 3, and 5 and decreases in the co-dominant, intermediate, and suppressed classes 2, 4, 6, and 7.
>
> "The results of this study emphasize the importance of marking for removal trees of classes 4, 5, and 7. It also indicates that perhaps more smaller diameter trees in classes 4, 5, and 7 should be removed than has heretofore been the practice. Class 3 trees are the safest risk where large trees are needed for seed or where reserve volume of valuable material is desired. Class 2 trees are a relatively poor risk and should be removed in preference to Class 1 trees where groups are to be thinned.
>
> "The selective thinning of stands with the removal of susceptible trees offer hope of greatly reducing the loss from insects, especially on the better sites."

This study also indicated a wide dispersion of mortality rates within certain tree classes and suggested that further subdivision of these classes might be helpful in segregating out the more susceptible types.

Keen tree classes.— In the hope of obtaining a more precise grouping of trees showing similar mortality rates or degrees of bark beetle susceptibility, Keen expanded Dunning's classification by using his basic conceptions of age, crown size, and dominance. Trees were divided into four primary age groups, i.e., Class 1, young; Class 2, immature; Class 3, mature; and Class 4, overmature; and into four crown-vigor groups, i.e., A- full, long, dominant crowns; B- full, shorter, co-dominant crowns; C- narrow, long, intermediate crowns; and D- short, narrow, suppressed crowns. The combination of four ages and four crown-vigor groups made a total of 16 classes possible (Figure 40 and description of age and vigor classes, Tables 4 and 5). Analysis of mortality occurring on 15,000 acres of sample plots in northeastern California and eastern Oregon between 1928 and 1931 showed that the highest proportion of losses was occurring in trees of poorest vigor, i.e. those of C and D crowns, and to a less marked degree in those of the older age classes 3 and 4. The first results of this study were published by Keen (67), followed by a later article (70) in which the characters separating the different classes were redefined and clarified after a detailed study of sample plots had indicated the characters most important in grouping trees of similar growth rates.

Figure 40 .— A ponderosa pine tree classification based on age and vigor.

(Page 381a follows)

A PONDEROSA PINE TREE CLASSIFICATION

BASED ON AGE AND VIGOR

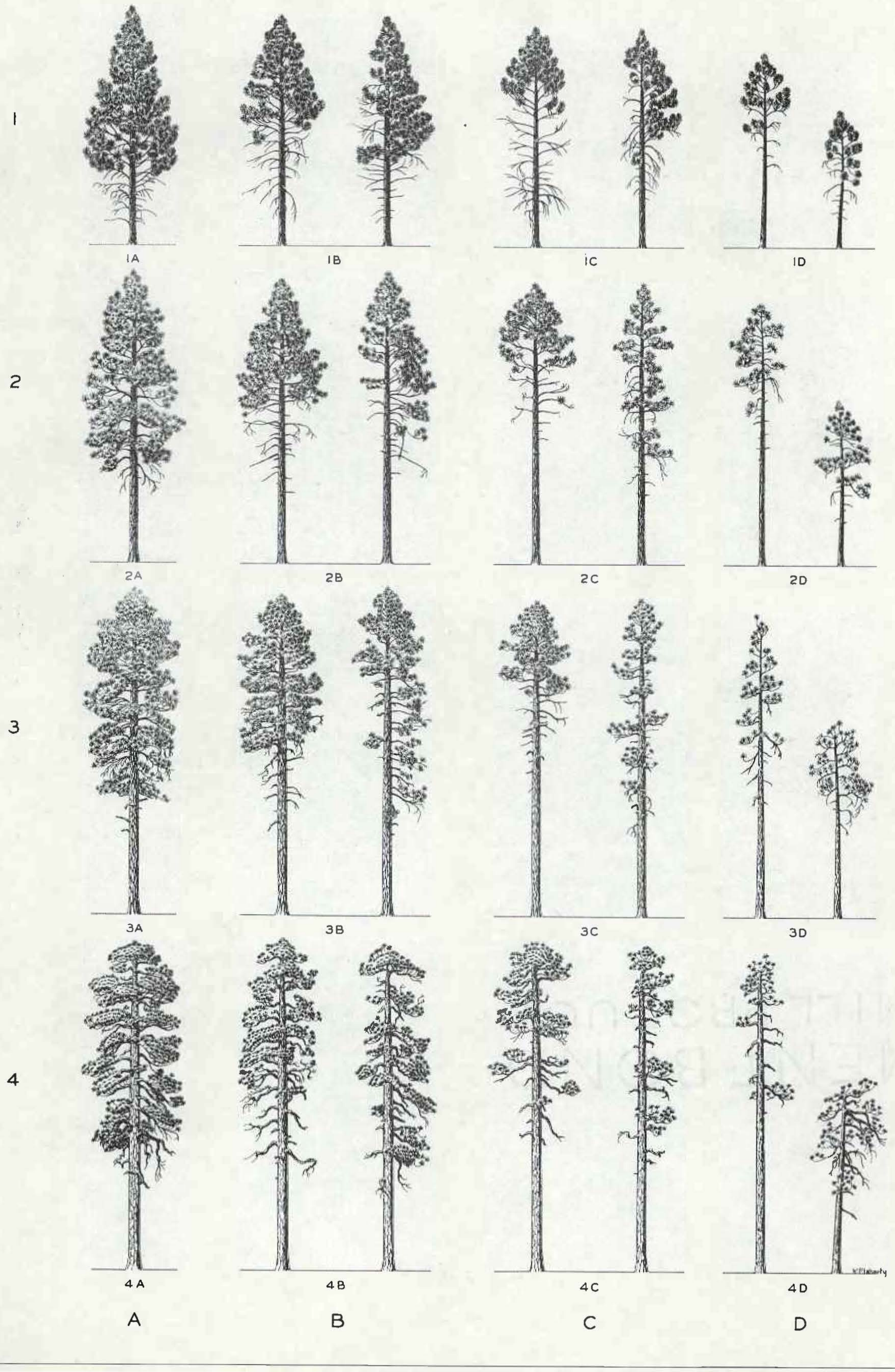

1
2
3
4
1A
1B
1C
1D
2A
2B
2C
2D
3A
3B
3C
3D
4 A
4B
4C
4D
A
B
C
D

Table 4.-- Description of Keen's age classes.

Character	Class 1	Class 2	Class 3	Class 4
Maturity:	Young	Immature	Mature	Overmature
Age:	Usually less than 80 years	Approximately 80 to 180 years	Approximately 180 to 300 years	More than 300 years
D.b.h.:	Rarely over 20 inches	Rarely over 30 inches	Rarely over 40 inches	Usually large diameters in dominant trees
Height:	In lower canopy usually less than 60% of total height of mature canopy	Height usually less than 90% of total height of mature canopy	Height practically that of general crown canopy (except of intermediate, suppressed or topkilled trees)	Full height of general canopy(except suppressed, spike-topped or broken tre
Growth and taper:	Thrifty trees making rapid height and diameter growth.Rapid taper.	Considerable height growth still in progress;good diameter growth in thrifty trees.Taper considerable.	Height growth practically complete;diameter growth slow. Moderate taper.	Making no height growth; diameter growth very slow. Least taper.
Bark color:	Dark grayish brown to black (except at extreme base)	Dark reddish brown on lower half of bole;dark bark on upper half	Light reddish brown on lower three-fourths of bole;dark bark showing in upper one-fourth of bole	Light yellow;uniform color throughout bole (except at extreme top)
Bark plates:	No plates.Rough bark, deeply furrowed,with narrow ridges between fissures	Narrow smooth plates between fissures	Moderately large plates between fissures	Plates usually very wide, long,and smooth;fissures often rather shallow
Branches:	Branches upturned in upper three-fourths of crown;small for diameter of bole	Mostly upturned in upper half of crown;lower half horizontal or drooping; small to medium for diameter of bole	Upturned near top;middle horizontal;lower ones drooping;moderate for size of bole	Large,heavy limbs,often gnarled or crooked;mostly drooping,except in extreme top
Whorls:	Whorls distinct in upper crown	Whorls distinct in upper half of crown	Whorls indistinct except at extreme top of crown	Whorls indistinct and incomplete
Top:	Top usually pointed	Top usually pointed, sometimes rounded	Top usually pyramidal or rounded,sometimes pointed	Usually flat,occasionally rounded or irregular

Note: Description primarily applicable to central and southern Oregon and northern California, Site IV

Table 5[illegible]-- Description of Keen's crown-vigor classes

Character	Class A	Class B	Class C	Class D
Crown vigor:	Full, vigorous	Good to fair	Fair to poor	Very poor
Crown length:	Long, 55% or more of total height; or less only if more than average width	Average length, less than 55% of total height (approximately 30% to 55% if full and wide), or a longer crown if narrow or somewhat thin	Short (from 10% to 30% of height, if crown of normal density) or long, sparse, and narrow	Very short (less than 10% of total height), sometimes merely a tuft at top of tree, or somewhat longer when sparse and ragged
Crown width:	Usually average width or wider (narrower if very long and dense)	Usually average width or narrower; may be flat on one side	Usually narrow or flat on one or more sides	Usually very narrow and sparse, or limbs all on one side
Crown density:	Usually full and dense or of medium density if longer than 55%	Usually of full to medium density, not sparse or ragged	Often sparse and ragged except at very top	Sparse and ragged
Foliage:	Needles of average length or longer, usually dense and thrifty	Needles of average length, usually dense and thrifty	Needles often short and thinly distributed, but of normal length and density when confined to top one-third of crown	Needles often short; foliag sparse or scattered or onl partially developed, but of normal length if reduced i quantity
Position:	Usually isolated or dominant, rarely codominant	Usually codominant; sometimes isolated or dominant; rarely intermediate	Usually intermediate; sometimes codominant or suppressed, but rarely isolated or dominant	Usually suppressed or inte mediate, but may occupy other positions if greatly reduced in vigor
Diameter:	Large for age	Average or above for age	Usually below average for age; sometimes larger in decadent trees	Decidedly subnormal for age, but very old, decadent trees may be of large diameter

Note: The descriptions apply to the usual types of trees found in each class; where exceptions occur, the size of living crown and amount of foliage are the primary considerations in determining the vigor class.

An analysis of 51,409 trees killed on 112,409 acres of sample plots during 1928-31, 1935-37, and 1939-40 as compared with 206,037 trees classified in a 10 percent cruise of 116,670 acres of sample plots in 1928-31, 1937, 1938, and 1939 showed the average mortality ratio of trees killed in the different classes to be as follows (70):

Average Mortality Ratios by Keen Tree Class in Virgin Forests

Age Class	Vigor Class				Average
	A	B	C	D	by Age
1	.1	.3	.8	1.1	.3
2	.2	.6	1.0	1.5	.8
3	.3	1.0	1.9	2.6	1.0
4	.4	1.4	2.7	3.8	2.1
Average by vigor	.3	.7	1.8	1.7	1.0

In connection with an intensive study of tree characters and development of risk symptoms, tree growth measurements were taken on a series of sample plots in eastern Oregon. These data were analyzed by Briegleb to determine growth rates by Keen tree classes and the results released by the Pacific Northwest Forest and Range Experiment Station in papers published in 1943 and 1945 (10, 11). This system of tree classification has come into general use for timber marking in most of the interior ponderosa pine type, where the objective is to remove the slow-growing beetle-susceptible trees from the stand and leave a fast-growing, resistant reserve.

Risk rating.-- Although tree classes were found to be a tremendous aid in differentiating between susceptible and non-susceptible trees in ponderosa pine stands, these systems did not entirely solve the problem of recognizing those trees most likely to be attacked at an early date. This was pointed out in an article by Keen and Salman (76):

> "While this tree classification indicates in a general way which types of trees in a virgin stand are most susceptible to bark beetle attack and therefore the kind of trees representing the highest risk of loss over a long period of years, it does not show which individual trees are likely to be killed within any short period of time. In fact, a considerable percentage of the volume killed each year may be in classes of intermediate risk and some loss may be expected even in the resistant classes."

Risk ratings were developed as a result of attempts to control beetles by light selective logging which would remove all of those trees most likely to become infested by beetles within a few years. Since the primary objective was control, it was desirable to make a cut no heavier than necessary to reduce the immediate beetle hazard. The problem requiring solution on the Black's Mountain Experimental Forest was explained by Salman and Bongberg (114) as follows:

> "When the Blacks Mountain Experimental Forest was established in 1934, a preliminary light sanitation cut which would remove a relatively small percentage of the total merchantable volume was planned by the California Forest and Range Experiment Station.
>
> "Foresters selected trees for cutting entirely on the basis of their high silvicultural undesirability. During the winter of 1934-35 serious infestations were found to be present throughout the experimental area and it was observed that the greater portion of the loss occurred in trees that had not been marked for removal in the sanitation cut....It became evident that special criteria should be used in the selection of trees if a light cut was to be successful in reducing losses due to insects."

The characters distinguishing four classes of risk in which all merchantable trees in the stands were grouped were first described in a memorandum by K.A. Salman (U275) and still further defined in a published article by Salman and Bongberg (114). (See Figure 41 and description in Table 6). A colored plate illustrating the risk classes was published by Whiteside in 1951 (138).

Figure 41.— Degrees of risk in ponderosa pine.

The characters used in separating trees into four risk groups of low, moderate, high, and very high risk were found almost entirely in the crown, particularly the color, density, and general thrift of the foliage. To a large degree these four risk groups paralleled Keen's four vigor classes A, B, C, and D, which also rated crown vigor largely on the basis of quantity of foliage, density, color, and general thrift. This similarity in the two systems caused a great deal of confusion at first, and still does. The difference is essentially one of distinguishing inherent vigor from current health. This is quite impossible to do for trees of normal vigor and health, but becomes important in recognizing those trees which are currently declining in health or are sick from one cause or another. Trees of highest risk were those in Risk 4 which were obviously in a poor condition of health as indicated by short, sparse, off-color foliage, and dead or dying twigs and branches.

Because the risk rating of ponderosa and Jeffrey pines had an immediate and highly practical application in current logging operations, studies were pressed from 1937 to 1943 to further define risk characters and to improve the methods of distinguishing high risk trees.

(Page 384a follows)

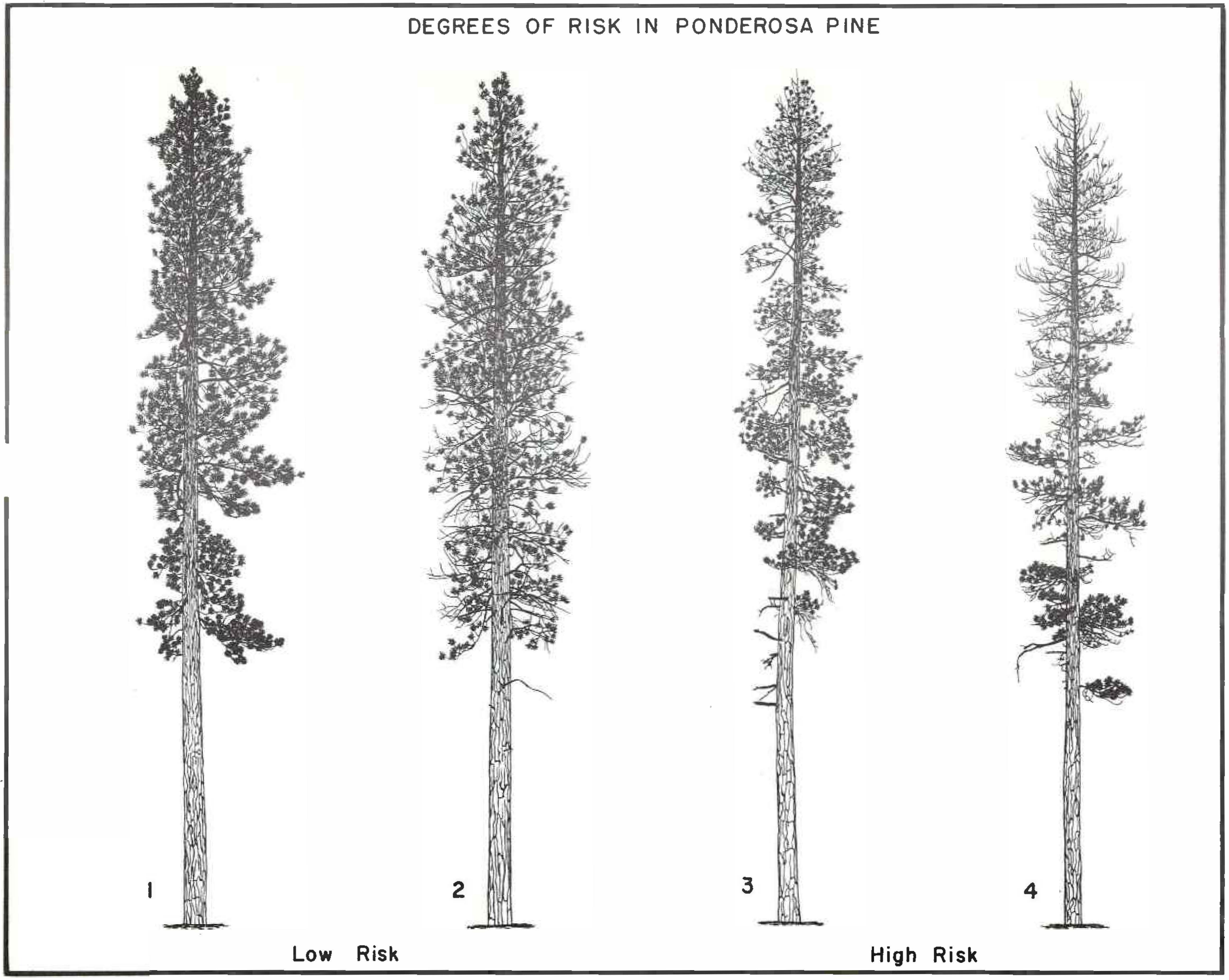

DEGREES OF RISK IN PONDEROSA PINE
1
2
3
4
Low Risk
High Risk

Figure 41.- Degrees of risk in ponderosa pine.

Table 6.— Descriptions of risk ratings

Risk I. Low Risk.

Full foliaged, healthy appearing crowns. Foliage of healthy appearance, needles usually long and coarse, color good dark green. Practically all twigs with normal foliage complement. No weakened portions of crown.

Risk II. Moderate Risk.

Fair to moderately healthy crowns, imperfect in spots. Foliage mostly healthy, needle length average or better, color fair to good. Some twigs or branches may lack foliage, but such injury should not be localized to form definite "weak" spots in crown.

Risk III. High Risk.

Crowns of fair to poor health, somewhat ragged or thin in portions of crown. Foliage in parts of crown thin, bunchy, or unhealthy, needles average to shorter than average in length, color fair to poor. Some to many twigs or branches lacking foliage, some to many twigs or branches fading or dead. Small localized weakened portions of crown usually present.

Risk IV. Very High Risk.

Crowns in poor condition, ragged or thin, often showing evidence of active insect infestations in upper portions. Foliage thin or bunchy, needles short or sparse, color poor. Twigs and branches dead or dying, portions of crown definitely weakened. Active top-killing or partial infestations often present.

In the first tests of risk rating on the Black's Mountain project in 1937, Bongberg (U23) found that high-risk trees were quite evenly distributed over the area, and were found in practically all diameter classes, but were more abundant in the predominating diameters of the stand.

Figure 42.--Painting spots on ponderosa pine to denote degrees of risk to western pine beetle attack. Black's Mountain Experimental Forest, California.

In further studies during the 1938 season Bongberg (U24) reviewed Salman's definitions of risk classes and attempted to develop methods for measuring the crown characters that denote risk, particularly the complement or number of fascicles per twig, and the length of the needles. He found that thin crowns of high-risk trees averaged 48 fascicles per twig, while dense crowns of low-risk trees averaged 121 fascicles. Needle length ranged from 4.2 to 7.1 inches.

During the 1940 season, Hall (U79) made a study of the physiological factors associated with crown decadence, based on eight trees and concluded that:

> "There are certain measureable factors in the crown of a tree which are indicative of marked decadence. These include greatly reduced twig increment for a period of about eight years, shortened needles, and fewer needle fascicles."

(Page 385a follows)

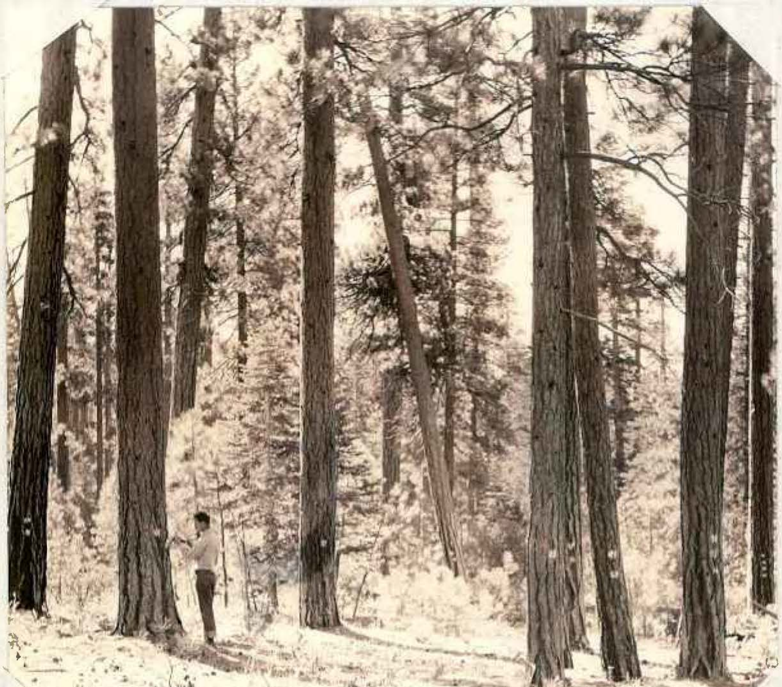


Figure 42.-- Painting spots on ponderosa pine to denote degrees of risk to western pine beetle attack. Blacks Mountain Experimental Forest, California.

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Salman (U278) found that risk ratings on the Blacks Mountain Experimental Forest were changed in 1940 by the effect of a needle cast fungus and the short 1939 needle growth. Subsequent studies have shown that risk ratings may change over a period of a few years as trees respond in health and vigor to changes in precipitation and other factors affecting growth.

A photographic study in 1940 by Charles Eaton (U52) showing the crown conditions in a series of trees on the Blacks Mountain area shows graphically the over-all appearance of the characters by which the four risk classes are separated. (See figure 41).

The measurement of risk characters was gone into quite thoroughly by Wygant (U328) at Blacks Mountain during the season of 1941. Seventeen high-risk trees and 16 low-risk trees were felled and analyzed to determine wherein the two groups differed as to needle length, needle diameter, needle retention, needle complement per twig, twig growth, and radial diameter growth. The more significant results brought out by this study were stated as follows:

> "The average needle complement per twig in the top and mid-crown of the risk 1 trees was 69 percent better than that on the risk 4 trees. This difference between the risk 1 and risk 4 trees was very highly significant, and between the risk 1 and risk 2 trees not significant. The variation in the number of needles per twig from tree to tree within each risk class was great.

"The average number of needles per twig was greater in the top crown than in the mid-crown by 5 percent on risk 1, 7 percent on risk 2, and 9 percent on risk 4....

"The average needle length in top and mid-crown of the risk 1 trees was 29 percent greater than on the risk 4 trees.... The variation from tree to tree within each risk class was great....

"The average annual twig growth in the top and mid-crown during the past 25 years of the risk 1 trees was 32 percent better than that of the risk 4 trees. This difference in growth was very highly significant. The variation from tree to tree within each risk class was great.

"Twig growth on the risk 4 trees has been on a decline throughout the past 25 years. While the growth on the risk 1 trees has been on somewhat of a decline during that period, the risk 1 trees have shown recovery since 1936 not shown by the risk 4 trees. At no time during the 25 year period did the twig growth of the risk 4 trees equal that of the risk 1 trees.

"The average annual radial growth during the past 30 years at the mid-bole of the risk 1 trees was 46.5 percent greater than at the stump. Mid-bole growth on the risk 4 trees was 11.1 percent less than growth at the stump. Literature on tree growth indicates that annual radial growth on the stem is normally greatest just below the living crown. Therefore the risk 1 trees were growing in a normal manner and the risk 4 trees were growing in an abnormal manner.

"Radial growth has been on a decline throughout the past 30 years. This decline has been greater on the risk 4 trees than on risk 1 trees. The risk 4 trees failed to show the improvement in growth that risk 1 trees have shown since 1936." (See Figure 43)

Figure 43 .— Comparison of annual radial growth of Risk 1 and Risk 4 trees.

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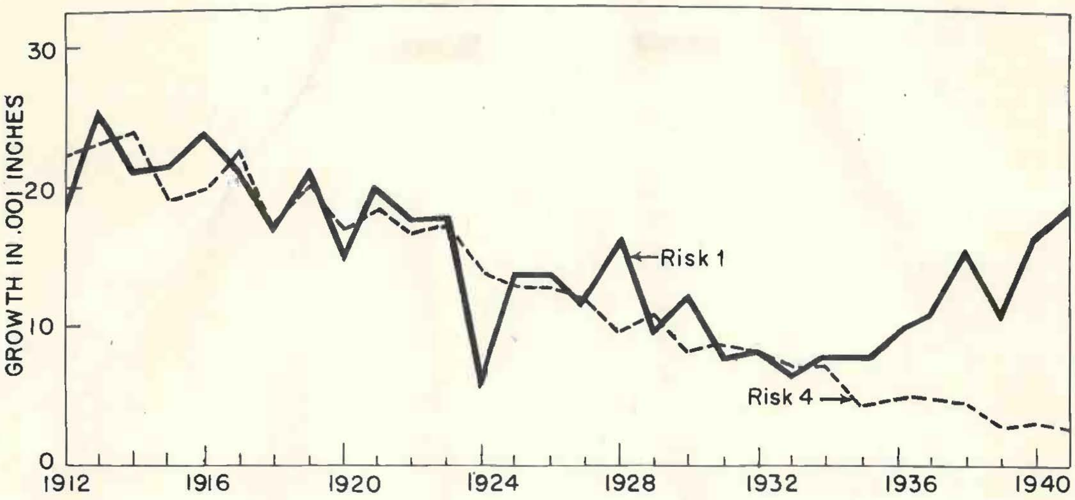
STUMP



MID BOLE

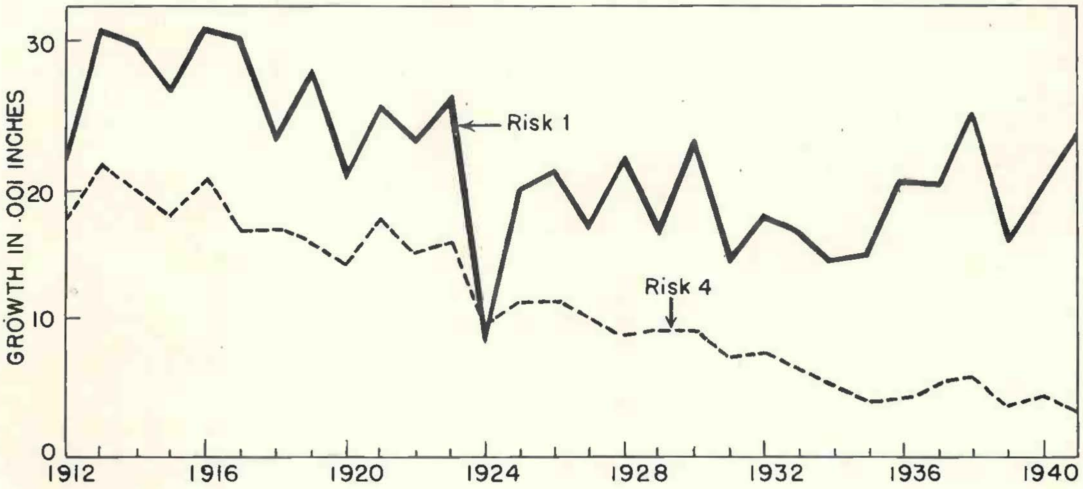


Figure 43.-- Comparison of annual radial growth rate of Risk 1 and Risk 4 trees.

The fact that Wygant found differences in twig growth and annual radial growth for periods of 25 and 30 years between the two groups of trees studied, shows conclusively that he was dealing with long time tree class differences rather than short term current health differences.

Wygant (U329) found that ocular estimates of needle complement per twig and needle length are subject to considerable error. In general appraisals were found to be between 64 and 68 percent correct. Apparently the appraiser is influenced in estimating needle length and needle complement by his general impression of the tree's vigor.

In the eastern Oregon areas, Bedard (U13) in 1940 made an analysis of the crown characters found in high-risk trees and found that:

> "Seven characters were found to be associated with high-risk trees. These were: (1)scraggly, scattered, open crown, (2) thin open top, normal or dense below, (3) very thin open crown throughout, (4) very short needles in top of crown, normal below, (5) new spike, newly broken top, or active area below an old spike, (6) medium wide active sapwood, and (7) abrupt growth declines with no recovery.
>
> "In analyzing these characters as to their origin and cause, it was found that Dendroctonus, Melanophila, cerambycids and fire scars were found frequently in high-risk trees, but not in normal trees. However, these factors were not in sufficient numbers,either singly or in combination, to be the primary cause of the decline.
>
> "The narrowed sapwood and general growth patterns of high-risk trees were believed to indicate a general decline in tree vigor resulting from a more general cause such as weather or soil."

By the close of the 1941 season, Bongberg (U28) was able to check the reliability of risk characters in 58 trees which had died, subsequent to risk rating, on 15 sample plots of the Black's Mountain area. He found that the following characters were highly indicative.

> "A sparse complement of needles in the top crown, in contrast to a more dense foliage below, is the most reliable and first in value as a character to be used in indicating high risk.
>
> "Short needles which were encountered in some of the trees, occurred primarily as a character dependent on the thin top crowns. Short needles alone were judged to be unreliable and of little value as an indicator of high risk.
>
> "Needles of an off-green color were not encountered in the trees which were killed without the association of a thin crown density. Poor colored needles, therefore, appear to be dependent on thin crowns. No appraisal could be made from the data avilable of the value of off-colored needles as an indicator of high risk.
>
> "The occurrence of dead twigs and branches in the trees which were killed was no more numerous than was its occurrence in the green stand.... From the analysis of data, it was indicated that severe branch and twig injuries are of limited value as indicators of current high risk.
>
> "Trees which had been top-killed occurred in greater proportion in the trees that were attacked than in the remaining trees in the green stand. It had been observed, however, that a progressive weakness often develops below a previous top injury and it is concluded that a top injury is of definite value as a character to be used in appraising high risk."

The following season, 1943, Bongberg (U31) reviewed the mortality that had occurred in high-risk trees on the Black's Mountain area during the period from 1937 to 1943. His material consisted of 557,300 board feet of ponderosa and Jeffrey pines which had been killed from one to six years after the trees had been rated according to risk. The records showed that most of the trees which had been killed were rated as risk 4 and were classified in the overmature class 4 of Keen's tree classes. It was also brought out that if all risk 4 trees were taken out of the stand, the remaining trees showed little difference in ratio of mortality by crown vigor classes. In his summary Bongberg stated:

> "By comparing the percent of risk class killed each year and for the entire period of record, with the percent of occurrence of the green stand by risk, it has been found that mortality ratios for each risk class are significant. This comparison also showed that the risk ratings are applicable to both ponderosa and Jeffrey pine under infestation conditions (annual loss) ranging from 0.03 to 0.99 percent of the green stand, and can be used in predicting future loss for at least six years... It was found that maturity was of little value as an added factor to ratings of risk to be used in predicting which trees are most likely to become attacked, but that the preponderance of risk trees occur in the overmature age classes.
>
> "The ratio of mortality or relative susceptibility of trees was found to be greatest in Keen's susceptible tree classes... Any increase in the accuracy of predicting which trees are most likely to be attacked and killed by beetles seems to be dependent on weeding out the crown characters indicating but temporary disturbances in tree health from those of significance as indicators of high risk and susceptibility, and in discovering other conditions not presently recognized as indicators of high risk."

In connection with the Rail Glade sanitation-salvage logging in the Bly District, Oregon, a nearby sample plot of 640 acres was set aside and high risk trees marked on it under the same rules as were used on the logged area. The purpose of the marking was to determine (1) what proportion of beetle-killed trees could be marked in advance of their attack, and (2) what proportion of trees marked for cutting would be actually killed over a five-year period. (U158).

Bedard (U21) summarized the first three years' results. These showed that 67 percent of the volume and 55 percent of the trees killed occurred in the approximately 15 percent of the stand marked as high risk. The remainder of the loss occurred in unmarked trees. The rate of loss in marked trees to total stand loss varied by years and by generations. It appeared that as infestation declines, a higher percentage of loss is found in high risk trees; while with higher levels of loss, more low risk trees are taken. In the three years' time, only about 10 percent of the marked trees had been killed.

This test showed that it was not always possible to select a high percentage of trees that might be killed by western pine beetle in advance of their attack, without selecting many trees which would survive. Even so, a higher proportion of selected trees were killed and the marking accuracy was sufficiently high as to indicate that the basic principles were sound. While only 67 percent of the volume of loss was predicted in the selection of risk trees under undisturbed conditions, the removal of such risk trees through sanitation-salvage logging is much more effective as a control measure than might be expected, and results in over 90 percent reduction in infestation. This is most likely due to the removal of "key" trees from groups and weak trees which serve to act as sources of infestation.

Variations in the reproducibility of tree classification systems.— Many trials have been made to determine how well different workers can reproduce the classification of a given set of trees on different occasions, and how well a number of trained men can classify trees in agreement with a standard. Trials have been run at ranger training schools, at spotter training camps, and in special tests between trained workers. The classifications which have been compared are Dunning's, Keen's and Risk.

The reproducibility of any classification depends upon the training and experience of the men using it, and the number of classes into which trees are classified as well as the preciseness of class definitions.

Keen's classification with its 16 classes offers the greatest chance for error in repeating the classification. But if this classification is broken down into the two primary subdivisions of age and crown vigor, each of which has only four subdivisions then a higher degree of reproducibility should be obtained. Dunning's classification with seven classes should represent the next most difficult classification to reproduce and the risk classification with four classes should be the easiest.

In 1941 Eaton (U53) compared the individual ratings of five men for the same trees on the same area and found that there was considerable variation in results. A plot of 100 trees was used as a basis on which each tree was classified visually according to Dunning, Keen, and risk rating systems. The ratings that were arrived at varied not only between individuals but also with the same man when he tried a second classification of the plot.

Eaton found the average frequency of agreement of the three most experienced observers in classifying the same trees on two occasions two weeks apart were as follows:

By Dunning - 78 percent agreement
By Keen - 82 percent agreement in age
72 percent agreement in crown vigor
60 percent agreement in both
By risk 73 percent agreement

The frequency of agreement of the three experienced men with a standard rating (the most expert man's first rating was considered standard) was as follows:

By Dunning:	83 percent agreement
By risk:	60 percent agreement

Eaton states:

> "The ability of a marker to classify trees uniformly varies with his experience... Ratings applied to the same tree by men of equal experience compare favorably, but untrained men cannot satisfactorily apply tree classes guided only by published descriptions of the systems.
>
> "Discrepancies in the tree class ratings made by different men may be accounted for by the fact that the discernment of the characters is not critical. Characters, like crown length, that may be compared against a standard, are more consistently rated than characters like twig injury, that cannot."

Rangers and insect survey crewmen at training schools in Oregon and Washington have frequently been tested to determine how well they can agree on rating a series of 100 to 200 trees by Keen's tree classification. ?

Percent Agreement in Keen Tree Class

Year tested	No. of trees	Men tested	By age	By vigor	Both age and vigor	
1935	73	37 rangers	73%	65%	50%	
1937	200	15 insect surv. crew	85%	90%	62%	✓ spell out
1939	200	12 insect surv. crew	86%	74%	63%	✓ spell out.
1939	200	3 B.E. & P.Q. ?	80%	70%	56%	✓
1943	100	3 B.E. & P.Q. ?	85%	80%	68%	✓

Experience has shown that tree age can be much more accurately judged than crown vigor class and that slight variations in either tend to operate against obtaining a high percentage of agreement when 16 classes are involved.

From all of the trials so far, the average reproducibility of Keen's classification and risk rating are as follows:

Keen's classification	
By age	80 percent agreement
By crown vigor	72 percent agreement
By both age and crown vigor	60 percent agreement
By risk rating	72 percent agreement

Relation to Silvicultural and Environmental Conditions

In addition to studies concerned with the characteristics of the host tree and its susceptibility or resistance to western pine beetle attack, several lines of investigation have been concerned with the influence of the environment and silvicultural characteristics of the forest stands in which most damage is found to occur. Climatic, edaphic, environmental, and forest stand factors have been studied for clues which would throw some light on the reasons for the rise and fall of epidemics. An understanding of these factors is basic to control of the beetle through forest management practices.

Climatic Factors

Precipitation.— To a very great extent the volume of seasonal precipitation determines the amount of soil moisture, which, as shown in Bedard's study, is the dominant factor in ponderosa pine growth. Since insufficient moisture limits growth and lowers tree resistance, it is only natural that periods of drought have been suspected as an underlying cause of unusual bark-beetle activity. Hopkins (43),however, was not impressed with the importance of this factor, since he included the western pine beetle in the following generalization: "Drought is not an important factor in contributing to the multiplication and destructiveness of this class of enemies."

On the other hand, Craighead (22) found a direct correlation between rainfall deficiencies and epidemics of the southern pine beetle.

The theory that drought, through its effect in lowering the growth vigor of trees, was similarly responsible for outbreaks of the western pine beetle was advanced by Craighead and others and was the basis for the extensive studies started by Keen in 1924 to determine the effect of climatic cycles on tree ring growth and epidemics of the western pine beetle in southern Oregon. (See p. 399).

Increasing ponderosa pine losses in eastern Oregon following 1924, while charged to bark beetle attack, were suspected of being primarily due to drought conditions and lowered tree vitality. These drought conditions were somewhat improved in 1927 and losses dropped the following year. Then more years of drought followed and reached a most critical condition in 1931 and 1932. The drought was so severe that A.J. Jaenicke (U100) reported much timber on the China Hat sale area of the Deschutes National Forest died primarily from drought. He stated:

> "As early as 1931 it was clear that the drought factor was important in weakening the timber in the China Hat sale area and increasing its susceptibility to beetle attacks, but it was not until 1933 that much timber began to die primarily from drought. The drought killing now (January 1935) overshadows the pine beetle problem and further beetle protection has little or no chance for success because of the drought problem. Nearly all of the drought-killed trees are attacked by the western pine beetle, engraver beetles, and flatheaded borers, before the cambium finally discolors, but these insects are playing a secondary role in the timber losses now in progress."

One of the first attempts to find a correlation between precipitation data and growth in nearby pine stands was made by Hauge (U87), working under Keen's direction. Hauge used the records of the U.S. Weather Bureau station at Klamath Falls, Oregon, and selected cores from a stand of ponderosa pine within a mile of the station. Although this study was preliminary and limited in scope, Hauge reached the following tentative conclusion: "In semi-arid regions there is a high degree of positive correlation between the amount of precipitation and the rate of growth in yellow pine."

Realizing that it would take many years of records to establish any evidence of cycles or any relation between precipitation and pine losses from bark beetles, Keen encouraged the continuation of plot loss records in the Klamath Basin of Oregon for over 30 years from 1921, for the purpose of studying their relationship as an integral objective of the yearly survey program. The trend of infestation in this area and the seasonal precipitation departures from normal at Klamath Falls, and Lakeview, Oregon, is shown in Figure 29 . While no direct relationship is shown, the heavy losses during the 1920's occurred during a time of general drought and the low losses since 1937 coincide with a more favorable precipitation period. A complete analysis of this long record is still to be undertaken.

Hall (U78) compared the average annual ponderosa pine loss from beetles on the Modoc National Forest plots with the seasonal precipitation at the nearest permanent weather station at Lakeview, Oregon, for the period 1921 to 1939 inclusive. He was unable to find any evident relationship and stated: "The correlation between precipitation and timber loss is far from clear cut."

A discussion of the relationship between precipitation and pine losses on the Sierra National Forest from 1909 to 1943 is found in a review of bark beetle investigations and control work by Miller, Struble and Hall (U199):

> "One characteristic of the association between precipitation and loss is that it is not specific in all years; i.e. a drought year does not necessarily mean a heavy loss year, as may be noted for the years 1912, 1924, 1934 and 1939. Neither does above normal precipitation mean low loss as may be noted for the years 1914, 1932 and 1935 (see figure 32). In studying these data it appears that precipitation effects are cumulative, either favorable or unfavorable, and that precipitation effects in any one year are dependent to a large extent on precipitation for at least two years previously.
>
> "Although it can be shown that there is an apparent relation between precipitation and beetle populations as represented by pine losses, it must be conceded that the relationship is not a direct one. Obviously dry weather in itself does not generate beetles spontaneously; drought must first have an effect upon the trees which creates favorable conditions for the beetles to multiply.

> "A comparison of tree growth (radial) and precipitation, as represented by the average growth pattern of a series of selected trees from the Cascadel basin and the Northfork weather record for the period 1912-42, indicates that...the effect of precipitation on growth appears to differ in different periods; here again, as in the loss picture, the precipitation effect in any one year seems to be dependent upon precipitation in preceding years... The above normal precipitation for 1932 followed eight years when precipitation had been below normal and appears to have had no effect in changing the growth trend which still progressed downward in 1933. These data seem to show that the prolonged drought from 1924 to 1931 was a serious shock to the trees and that recovery after this drought was comparatively slow. From 1912 to 1931 the precipitation percent of normal was below the growth percent of normal in 17 out of 20 years; after 1931, however, the precipitation curve was above the growth curve in ten out of eleven years.
>
> "In general it can be claimed that beetle-caused losses are inversely related to the growth rate... A steadily declining growth rate over a period of several years prior to 1930 was followed by a very rapid rise in the loss level; on the other hand, the general rise in growth rate from 1934 to 1940 was accompanied by a fluctuating, but nevertheless, substantial lowering of the loss level."

Climatic cycles.— One phase of the ecology of the western pine beetle which has received quite thorough investigation is the relation of tree ring patterns to climatic cycles. Since it is generally accepted that several seasons of suppressed radial growth in pine stands are usually followed by periods of accelerated bark-beetle activity, the regularity with which years of suppressed growth have occurred in the past should give a clue to the expectation of bark-beetle losses in the future. Whether or not there is a rhythmic cycle of favorable and unfavorable growth years should show up in tree ring patterns.

The tree ring record of the pine stands of eastern Oregon and northeastern California was intensively studied by Keen (68). Interest in this line of investigation was stimulated by the prolonged droughts accompanied by increasing bark-beetle infestations during the years from 1917 to 1933. The application of the study was defined by Keen:

> "The question naturally arose in the minds of foresters and timber owners as to whether this trend toward dryness and the retreat of the forest was to continue over any long period of time or was merely a short cycle in a variable climate which would soon reverse the trend and give some hope for forest perpetuation in threatened sites. Since this problem was intimately tied in with increasing timber mortality due to bark beetle activity, we as entomologists were concerned to know whether we could expect any eventual aid from Nature in holding beetle damage in check."

In Keen's preliminary paper (68) micrometer measurements of annual radial growth in 1,240 ponderosa pines from 44 different localities in eastern Oregon covering a period of 650 years were treated by statistical methods and served as the basis for the following conclusions:

> "A significant correlation was found between seasonal precipitation and tree growth. On comparing the cumulative effect of two years of precipitation with tree ring growth, a highly significant correlation was found. By taking into account the distribution of rainfall through the year and the cumulative moisture through several seasons, an even higher degree of correlation may undoubtedly be found.

> "The tree ring record for eastern Oregon indicates that during the past 650 years there has been no general trend toward wetter or drier years. If such a trend exists, the change over a 650-year period is so slight that it is obscured by other fluctuations. Average growth for the 20-year period 1900 to 1919 was found to be identical with the average growth during the past 650 years. There have been important fluctuations of growth throughout the entire period, however, with alternate periods of good and poor growth.
>
> "All tree ring measurements agree in showing that a very critical subnormal growth period has existed since 1917. This slowing down of growth rate is undoubtedly the result of deficient precipitation and lowered water tables. As compared with other drought periods, the present one is the most severe and critical that the present forests have experienced in the last 650 years. Several other periods have exceeded the present one in duration of subnormal growth, but none has approached it for severity. Growth in 1931, the poorest year, was 68 percent below normal.
>
> "The tree ring record indicates that the last period of 19 years of drought and poor tree growth represents a major fluctuation in a broad climatic cycle which will eventually be followed by a wet period of better than average growth. No rhythmic cycle has been found which would permit a prediction as to when this reversal in trend will occur."

This article of Keen's was published just before a series of wet years which began in the pine type areas in 1938 and which have continued without interruption by drought years up to and including the winter of 1944-45.

Light and temperature.— The three-way relationship between precipitation, growth rate, and western pine beetle losses is apparently too complex to be stated by any simple formula. Other natural factors may influence growth rate and obscure the effects of precipitation, even though soil moisture may be the dominant factor. Favorable light and temperature conditions are essential to normal growth. Low temperatures may inhibit growth in years even when precipitation is abundant. But the list of publications and reports to date reveal but few attempts on the part of forest entomologists to link the light and temperature factors into the chain of climatic influences which produce favorable growth conditions for the tree and indirectly increase its resistance to barkbeetle attack.

In connection with the periodicity of epidemics of the western pine beetle in southeastern Oregon, Keen analyzed seasonal temperature departures in an attempt to determine whether the incidence of epidemics was associated with abnormal temperature conditions. Nothing of any significance was uncovered in this study.

Hall (U77), in his study of climatic factors, has found that zones of highest hazard from bark-beetle attack are those where low precipitation, high temperatures, and rapid evaporation all combine to decrease available soil moisture, but the temperature effect has not been isolated from other factors.

Phenological events.-- In principle, phenology deals with the timing of biological events such as the opening of buds, emergence of insects from hibernation, or the subsidence of insect activity in the fall, as related to latitude, longitude, altitude, and topography. It has been assumed that the difference in timing of such biological events between localities can largely be accounted for by differences in these basic factors.

Hopkins (44,45,46) developed what is known as "Hopkins' bioclimatic law" which states that other conditions being equal, the variation in time of any seasonal biological event in temperate North America occurring in the spring and early summer is at the general rate of four days later for each degree of latitude northward, or five degrees of longitude eastward, or 400 feet of altitude upward. In late summer and fall, conditions are reversed. This law has been applied with some success east of the Rocky Mountains, but does not hold too well in the mountainous regions of the West.

Under the guidance of Dr. A.D. Hopkins, the Ashland station collected a large amount of data pertaining to phenological events in the ponderosa pine type of the Rogue River area from 1914 to 1918. These records consisted mainly of noting the time when certain plant activities occurred, such as opening of buds, flowering, fruiting, and dormancy, at fixed stations. These phenological records were kept in connection with seasonal history records of the western pine beetle. It was hoped that from this study it would be possible to use the phenological events of certain plants as a key to the seasonal activity of bark beetles within the same area.

All of these records were transmitted to Dr. Hopkins, who published (44) on the effect of altitude on beetle emergence (see page 153) but did not include the records of plant activity as correlated with the beetles' seasonal history.

In the western pine areas, attempts to find a fixed relationship of plant and insect activity to elevation, latitude, and longitude have broken down or at least have found such a relationship too complicated for practical use. In these areas there are many factors which modify the temperature conditions which control plant and insect development. Slope and exposure are important and these two factors, together with the modifying effect of topography upon moist air currents from the Pacific, create a very complex set of influences which do not lend themselves to simple analysis.

The Ashland phenological records emphasized the extent of the departures from the theoretical constants of the bio-climatic law when applied to the varied climatic conditions of the Pacific Coast pine region. In comparing the emergence of _D. brevicomis_ at elevations of 3200 and 5700 feet, the theoretical difference was figured out to be 25 days, but the actual emergence records showed a difference of about 50 days.

What is known about the effects of altitude, latitude, and longitude upon western pine beetle development is discussed under seasonal generations in Section II , pages 153-156. No fixed relationship of western pine beetle activity to these factors has been established, mainly because their effect is obscured by wide climatic and seasonal variations between localities within the range of the beetle's distribution.

Environmental Factors

Elevation.— Forest entomologists have frequently noted that there appears to be an altitudinal range most favorable for the western pine beetle. This range roughly coincides with the altitudinal range of the host tree. Below this range and above it, conditions do not appear to be favorable for western pine beetle infestations.

Miller and Person (U183) were unable to establish broods in a pine stand 1000 to 1500 feet below the true ponderosa pine type in the southern Sierras. Usually epidemics are limited to the ponderosa pine belt below the 5500 foot contour in this same region, even though a few ponderosa pines may be found at higher elevations.

Keen (U150) used elevation as one of the criteria of hazard to bark beetle attack, based on the observation that the western pine beetle was less active and had fewer generations at the upper, colder altitudes than in the optimum range (see page 425).

Hall (U77) found in 1939 that average daily air temperatures were approximately six degrees colder in the upper ponderosa pine zone at 5000 feet than in the lower zone at 3000 feet on the Burney area of northern California. Due to differences in temperature, the upper zone produced two and a quarter generations a year while the lower zone had three and a quarter generations.

Elevation, due to differences in air temperature and soil moisture conditions, which are reflected in tree growth and resistance, is thus definitely correlated with degrees of hazard to bark beetle attack.

Slope and exposure.— Struble (U287) stated "slope and exposure are important in limiting moisture supply during an epidemic year, and influence the beginning of an attack in one locality in preference to another."

Salman and Johnson (U271) compared losses on north and south exposure and on slopes, flats, and ridges. They found that southern exposures were slightly more susceptible to losses than northerly exposures. The susceptibility indices were 1.08 to 0.92 respectively. They found considerable difference between slopes, ridges, and flats. Ridges were found to be most susceptible with an index of 1.95; slopes had an index of 1.40 and flats had the least loss with an index of 0.75.

Soil conditions.-- The extent to which soil conditions may influence growth vigor and indirectly the susceptibility of ponderosa pines has been given only slight attention in western pine beetle studies. Bedard found that most of the literature regarding the texture and structure of forest soils was confined mainly to hardwoods and that comparatively little is known about the soil requirements of ponderosa pine.

In 1928 Keen collected samples of the characteristic soils in the eastside pine type of northeastern California for analysis of their moisture holding capacity by the Soils Department of the University of California. The results of this study were negative and never were written up in report form.

Further investigationsof soil conditions were begun by Hall (U77) in 1938 as one phase of a general study of the influence of climatic and edaphic factors upon timber losses in the eastside pine stands. Hall considered the main soil factors affecting tree growth which could be measured in this area to be (1) soil temperature and (2) soil moisture at varying depths up to 16 inches. Only one progress report (U77) on this study has been made available to date. Preliminary results indicated that "soil moisture at a depth of 9 inches was significant of the degree of beetle hazard, but that moisture at the surface and at a depth of 16 inches was not; soil temperature was apparently related to hazard."

Studies by Bedard in 1941 (U17) dealt with the effect of irrigation on the radial growth of ponderosa pines. From a series of 13 irrigated and 13 non-irrigated trees he concluded that: "Irrigation increases the radial growth of ponderosa pines in years when precipitation is insufficient to supply normal moisture requirements."

However, the radial growth on the trees which Bedard irrigated during the season of 1940 was no greater than in non-irrigated trees on the same site which would indicate that these trees received sufficient moisture without irrigation.

In 1942 and 1943 Bedard went still further into the soil requirements by making an analysis of the chemical and physical properties of the soil upon the growth of ponderosa pines. On small experimental plots he controlled the amount of water, determined the wilting coefficients, and added nitrogen and phosphorus to test the effect of varying amounts of these materials. His summary (U22) of the results of these experiments included the following statements:

> "Nitrogen affected top growth with increase in leader length, needle weight, needle complement, and top radial growth. Phosphorus resulted in increased twig elongation, needle length, needle weight, and both basal and top radial growth. In general these nutrients increased top growth and apparently tended to inhibit root growth - at least tops increased more in proportion than roots.

> "Water was the most dominant factor in these tests. An insufficient supply resulted in significant decreases in total growth. An optimum supply caused increased growth in twig elongation, needle complement, and basal radial growth. An additional supply above the optimum caused no additional growth increases. Water at or above the optimum did, however, cause tops to increase more in proportion to the roots."
>
> "The combinations of water and fertilizers showed no significant interactions generally except in a few cases when the component parts of the combination strongly supported or opposed each other. Nitrogen and water decreased top radial growth below the effect of nitrogen alone. Phosphorus and water decreased top radial growth but increased basal radial growth. The combination of all three shows these same interactions plus an additional increase in top over root.
>
> "Soil treatments had no effect on the growth period of shoot, needle, or cambium except that water in insufficient quantities shortened the growing period."

Forest Stand Factors

It has been repeatedly observed that certain ponderosa pine stands are much more susceptible to western pine beetle attack and repeatedly suffer heavier losses than do other stands. Some areas over a period of years have cumulatively lost 90 percent of the original stand volume while nearby areas have suffered little or no depletion. The reasons for these differences have been the subject of much speculation, many theories, and some critical analyses of area and stand hazard factors.

Site.— Differences in site were early suspected of accounting for differences in western pine beetle damage as between various forest stands.

Site is defined by the Committee on Forestry Terminology of the Society of American Foresters (38) as "an area considered as to its ecological factors with reference to its capacity to produce forests or other vegetation, the combination of biotic, climatic, and soil conditions of an area." Site is theoretically a combination of those factors, just discussed, which when favorable enable the tree to produce vigorous growth and resist beetle attack.

No completely satisfactory method of measuring site has been worked out for ponderosa pine. The standard practice has been to measure "site quality" by the height which mature trees normally reach, while "site index" is determined by the height which trees reach at the age of 100 years. But these measures of site do not adequately integrate all the ecological, biotic, climatic, and soil factors of an area, and as a consequence, site and beetle behavior are not strongly correlated.

In general, it has appeared that over long periods bark beetle losses are heavier on low quality sites and relatively light on high quality sites, at least in terms of percent of stand killed. Some preliminary data were collected by Person (104, U228, U233), who concluded that: "In general poorer sites with open pure ponderosa pine stands along ridges or on exposed locations are preferred by D. brevicomis."

In 1928 Keen (U140) made a study of the susceptibility within the Dunning tree classes of some 10,053 green and 13,160 beetle killed ponderosa pines and analyzed the selection of these trees in relation to site. His conclusions were:

> "Poor sites show a greater loss than good sites. On the poorest sites the selective tendency is less marked, the trees of all classes being reduced to such a low stage of vigor as to become susceptible to attack. On good sites there is a marked selection of the suppressed and co-dominant trees of (Dunning's) classes 4 and 7. As the site becomes poorer the proportion of loss increases in the dominant classes 1, 3, and 5 and decreases in the co-dominant, intermediate, and suppressed classes 2, 4, 6, and 7."

In 1935 Keen (U148) summarized the loss records from 15,680 acres of sample plots cruised in southern Oregon and northern California during the 12-year period 1921-32 to show the distribution of loss by sites with the following results:

Beetle Losses in Relation to Site Quality

Site	Average Net Loss Per Acre Per Year - Board Feet	Average Percent Stand Killed in 12 Years
3-	175	10.8
4 +	232	14.6
4	298	27.8
4 -	280	34.0

In commenting on the significance of these data, Keen states that the above table:

> "indicates that insect losses bear a definite relationship to site quality either directly or indirectly. The percent of stand killed increased with a decrease in site quality. The net loss in board feet per acre, however, was somewhat lighter on Site 4, because of the smaller volume of the stand on such sites.
>
> "And yet, the above averages only tell a part of the story, for in some cases relatively poor sites have shown very low losses, while some good sites have sustained extremely high losses. The rate of tree growth and the degree of individual tree vigor is frequently independent of site quality and appears to play an important part in determining susceptibility in any particular stand. It is necessary, therefore, to look further than site quality for an index of bark beetle selection tendencies."

Salman and Johnson (U271) in their 1936 study of hazard factors in northeastern California, found Site II to have a susceptibility index of 0.93, Site IV with an index of 0.88, and Site V with an index of 1.27. They state: "The surprising thing about the susceptibility indices for the three sites represented in the sample is the relatively small spread between the indices for the markedly different conditions."

In 1937 a 10 percent count of snags was made on 174 half-section plots throughout eastern Oregon and Washington which gave the following comparative loss on different sites:

Pine Beetle Damage by Sites

Site Quality	Number Plots	Total Snags	Average Snags per Acre
II	2	980	1.5
III	16	13,000	2.5
IV	137	109,420	2.5
V	19	17,300	2.8
	174	140,700	2.5

This comparison shows very little difference in average number of snags per acre for the principal sites III, IV, and V, when a large forest region is involved. The comparison by percent of stand represented by snags would have shown wider differences by sites. Apparently other factors, such as stand density, local precipitation, and infestation conditions play a more important part in determining the intensity of losses than does the factor of site alone.

One multiple correlation analysis made by Keen (U149), using 25 full section plots in the Klamath Basin and their record of ten years of losses, showed a simple correlation coefficient between mortality and site index of -.65 which means that in this case 42 percent of the variability in losses was associated with site index, but a partial correlation and "t" test showed that site had no significance in explaining losses when taken alone. In reference to this Keen states:

> "At first thought this is most surprising. We have been thinking of site and growth rate as highly important in explaining variation in losses and by this test they each fail to show significance.
>
> "The reason for the failure of site index to show significance is partly due to the lack of spread in this case. Nearly all the plots ran to site quality IV and the total range in site index was only from 70 to 100. It is unreasonable to expect a variable which is nearly constant, to explain any large part of the wide variation in losses. In the second place, site is at its optimum in the middle of the pine belt and decreases at both higher and lower elevations. Beetle losses increase at the lower elevations, but not at the higher and hence do not move together with changes in site."

In 1943 Bedard (U18) completed the analysis of a one-acre plot study started by Keen in 1938 in which past ponderosa losses in terms of percent of stand killed were compared with various environmental and stand factors. He found no relationship to site even in the simple correlation tests.

The conclusions reached from all of these studies are that while heavy losses are frequently associated with the poorer sites, this is not due to site as such but because poor sites are more frequently associated with other factors more directly responsible for insect damage.

Volume per acre.— The volume of timber per acre is another measure of site. In general, poor sites have low volumes while good sites have high volumes per acre. This factor has been considered as an index to stand hazard by a number of workers, as it has been noted that in general stands of low volume have suffered heavier losses than those of high volume.

In each of the multiple correlation analyses made by Keen (U149), Keen and Grant (U154),and Bedard (U18), this factor showed strong negative relationship with stand mortality. Johnson's data from northeastern California showed the same strong correlation between stand volume and beetle hazard zones (55). Stand volume was used empirically by Keen (U149) in hazard zonation work.

Susceptible volume.-- It is reasonable to expect that stands with the highest percentage of volume in susceptible trees should show the highest hazard to continuing beetle damage. Several multiple correlation analyses by Keen and Grant (U154) in which susceptible volumes by Dunning's and Keen's tree classes were tested, failed to show this factor as having any significant positive correlation with loss. This was probably due to the strong positive correlation of susceptible volumes with total volume per acre. In Bedard's study of one acre plots (U18) the percent of susceptible volume showed an almost significant positive correlation with loss. Since such a low order of relationship was found between susceptible volume and loss, this factor could not be used in hazard analyses.

Up to the date of this writing, correlation studies to test the relation of percent of high risk trees, as defined by the California risk-rating system, to insect-caused losses, had not been made. The general evidence indicated that this factor was of definite significance as an indicator of hazard and it was used empirically in the hazard zonation work in California reported by Johnson (55) and in subsequent hazard zonation work in Oregon.

Forest type.— Forest type usually changes with elevation and life zone. Ponderosa pine is characteristically a transition zone species. At the fringe of the pine belt at lower elevations, it is often found in mixtures with mountain mahogany, juniper, and oak. Heavy losses of pine from beetles are frequently found in this fringe type (U256). Pure stands of ponderosa pine, occurring in the middle elevational zone are also often subject to heavy damage. At the upper elevational zones, the pine type runs to mixtures with white fir, lodgepole, and other species. In these types, beetle damage is usually low, but may be high if these other species are competing seriously with pine for light and growing space.

Salman and Johnson (U271) found a low rate of loss where white fir was mixed with ponderosa pine stands in Lassen County, California, and a very high loss where incense cedar occurred in the mixture. They showed that the average percent of stand killed in 10 years by forest type was as follows:

Type	Susceptibility index	Average percent stand killed
Ponderosa pine - white fir	0.68	21.4
Ponderosa pine	0.72	19.8
Ponderosa pine - Jeffrey pine	1.01	25.6
Ponderosa pine, Jeffrey, incense cedar	2.02	33.4

It stands to reason that no forest type can be permanently more susceptible than another without the pine ultimately disappearing from such a type. Therefore, the hazard of any forest type varies with time and other forest conditions currently prevalent.

Density.— Bedard (U18), working with one-acre plots, failed to show any significant relation between past loss and density of ponderosa pine, either stems or basal area per acre. Good sites have more stems per acre than poor sites. Johnson (55) showed a higher stand density on better sites, where the past loss and beetle hazard ratings were low. The indications are that stands tend to be in balance with their environment. Only where sites have more stems than the ground can support would one expect to find heavy losses. This sometimes occurs in stands with a heavy understory of reproduction, either pine or fir.

Competition.— Competition of brush, reproduction, or understory trees with mature pines has often been suspected of causing a weakening of the mature stand and increasing its susceptibility to loss. Bedard (U18) in analyzing data from 139 one-acre plots in southern Oregon found significant positive correlations between loss and the percent of ground covered with brush and a highly significant positive correlation with a competition index consisting of the percent of ground covered by reproduction times its average height. But because of great variability of competition on larger areas, this factor has not been found to be useful in hazard zonation work.

Growth.-- Since it has been shown that the growth rate of trees is a good indicator of their resistance or susceptibility (pp. 336), it was suspected that the relative growth rate of stands might be a measure of their hazard to beetle attack. Briegleb (9) in studying selectively cut stands in Oregon and Washington, found mortality, although variable, could be related to and computed from gross annual growth per acre in board feet. The relationship was curvilinear.

Keen (U149) found a highly significant simple correlation of -.76 between percent of stand killed and normal volume of growth on a study of 25 full-section sample plots in the Klamath Basin of Oregon. He also found the percent reduction in growth, which increment cores showed for the past 10 years as compared with the previous normal, was highly significantly correlated with loss. In fact it was the one outstanding factor indicating hazard when the partial correlation coefficients were tested.

Growth reduction also showed a high significance as a factor of hazard in the multiple correlation studied by Keen and Grant (U154) and was one of the important factors used by them in the construction of an alinement chart to determine hazard.

Cut-over lands.-- Since cutting of timber stands affects density, competition, growth, volume per acre, and the percent of susceptible volume left in the reserve, it is reasonable to expect that cutting will have a profound effect upon bark beetle damage.

Salman (U261) made a study of cut-over lands in the ponderosa pine type of California and found that except for the lower volume of loss, the losses on cut-over lands followed the same general tendencies as in virgin stands. There was no marked change in the insects primarily responsible for loss. Losses were heavier on poor sites than on good sites, and heavier in pure pine stands than in mixed type. There seemed to be no relation of loss to methods of cutting, with diameter distribution or reserve volume. Losses were lighter on plots where the increment was high.

Yearly cruises of cut-over lands have shown that volume of loss is greatly reduced by cutting, but that the percent of stand killed per year may not vary greatly from nearby virgin areas. The trend of losses on cut-over lands follows the same trend as in virgin stands of the same locality.

The effect of different methods of cutting in controlling pine beetle losses is further discussed on pages 694 to 724.

Hazard Zonation

All of these factors discussed above are difficult to isolate and are so interrelated in their operation upon bark beetle infestations that forest entomologists have not been able to deal with them separately. Instead the term "bark-beetle hazard" has been used to designate the net result of all factors that contribute to the expectancy of western pine beetle infestations within an area. Under the heading of hazard studies, quite a large amount of work has been done and a number of reports prepared dealing with the different degrees and causes of bark beetle hazard in ponderosa pime stands.

The ideas underlying bark beetle hazard apparently originated in observations that certain areas were much more subject to recurrent losses than others and seemed to occur in well defined zones. It was fairly obvious that site quality alone did not explain this differentiation of high and low loss areas; the age of stand, forest type, elevation, and various other factors could be used as equally suitable explanations. Nevertheless, it was believed that if pine stands could be classified, mapped, and inventoried according to the degree of hazard from beetle attack, the information would be of immediate value in forest utilization and management plans for specific areas.

The first attempts in 1936 to classify pine stands according to the degree of susceptibility to bark beetle attack approached the problem on a purely empirical basis. Salman and Johnson (U271) ran sample surveys on a series of eastside areas in the Lassen and Modoc National Forests to see if the physical characters of the stand would serve as indices to the rate of past, current, and expected losses; and also to find out what practical difficulties would be involved in surveys to classify areas by degrees of hazard. The factors taken into account in this attempt to recognize beetle hazard included stand volume per acre, timber type, site index, exposure, slope, relation of current to past losses, and thrift of trees as expressed by Keen's tree classes. It was found that the operation of all these factors was too complex to permit of any simple method of weighing them in terms of beetle hazard. Among the conclusions reached in these preliminary studies were the following:

> "It seems possible to secure a quantitative estimate of hazard by measuring the past loss if that measurement includes those that have occurred over a relatively long period of time.
>
> "The relative hazard also can be determined if one is experienced and has an intimate knowledge of past conditions by a visual estimate that takes into consideration the loss and certain gross environmental indices.
>
> "A combination of visual estimates and selected measured samples seems to be the more practical and satisfactory basis for securing a hazard rating.
>
> "An adequate quantitative and qualitative basis for rating hazard may be secured on a (1)general (subregional), (2) a fairly specific (environmental unit), or (3) a very specific (local environmental) basis. The second unit of estimate seems to be best adapted for the application in forest-management practice." ?

From these studies Salman and Johnson set up five classes of hazard ratings grading from very low to very high and developed methods for sampling and rating pine areas under this classification. These were the methods used for the hazard inventory of the northeastern California pine stands which was started in 1937 and completed in 1940. The purposes and methods of this survey have been described by Johnson (U120) in Part II of the Hazard Inventory Report, and in an article describing the survey (55). According to Johnson:

> "The immediate objective was to find criteria which would (1) indicate beetle hazard directly or serve as an element in determining hazard, (2) provide a basis for arithmetically determining hazard ratings for any and all pine stands, (3) be easily obtained under normal field conditions and by average skilled forest technicians, and (4) allow the inventory to be completed within the time and fiscal allotments set up for it.

> "A number of factors bearing on the current beetle hazard of pine stands were studied, but only two were found which were significant and which fulfilled the requirements listed above. These were (1) the percentage of the pine volume previously killed by bark beetles and (2) the percentage of the present pine volume occurring as high-risk trees."

This article describes the field methods of sampling to determine the volume of the two indices defined above, and the computations used in determining the hazard ratings for the different areas.

In 1938, a series of studies was started by Keen in the eastside pine stands of Oregon to determine by methods of statistical analysis, the principal indicators of hazard and the weights which should be given to each of the more important factors. The objective was to find a sound basis for making hazard zonation appraisals.

In 1939, Keen (U149) with the aid of R.C. Grant, made a multiple correlation of ten years of loss on 25 full-section sample plots in the Klamath Basin of Oregon with site index, volume per acre, volume of growth per acre, and growth reduction percent. Highly significant simple correlations were found between loss rate and all of these factors. A regression equation was developed which bombined these factors, and which explained 51 percent of the variance in current loss. Of these factors, growth reduction was the most important and the only one to show significance in partial correlation tests.

In 1941, three more statistical analyses were made by Keen and Grant (U154) using data from the regional survey plots. Two different sets of data were used, combining different sets of factors. In the first analysis, data from 25 full-section Klamath Basin plots were used. Mean annual loss for the 10-year period 1931-40 (called "future loss") was correlated with past loss for the 10-year period 1921-1930, susceptible volume by Dunning's classes and radial growth reduction percent. This showed a highly significant correlation between future loss and past loss and a highly significant negative correlation between future loss and susceptible volume per acre, but no significant correlation between future loss and past growth reduction.

The next analyses were based on data from 114 plots of 320 acres each scattered through eastern Oregon and Washington on which a stand inventory and snag count had been made in 1937. In these analyses future loss, measured after the cruise, from 1937 to 1939, was correlated with past loss (before 1937), susceptible volume, total volume per acre, and growth reduction. It was found that future loss was significantly correlated with volume per acre, and 1936 growth reduction, and highly significantly correlated with past loss. Past loss was responsible for fully half of the explained variation of 41 percent.

Using the most significant factors shown from these analyses, Keen and Grant developed a regression equation and alignment chart combining past loss, volume per acre, and percent growth reduction to obtain an estimate of future loss in terms of percent of stand killed annually. Data was not available to include the factor of percent of risk trees, which from the California studies was thought to be highly significant.

Another approach to the determination of area hazard was started in 1938 and 1939, when insect survey crews working under Keen's direction in southern Oregon established 139 one-acre plots and took various data on loss and stand conditions. These data were analyzed statistically by Bedard (U18),who summarized the results as follows:

> "In the analysis of these one-acre plot data, 16 independent variables were correlated with the mean annual insect loss expressed in percent of stand killed, and it was found that the amount of ground covered with brush showed a significant positive correlation with current loss; the amount of ground covered by reproduction multiplied by its average height showed a highly significant positive correlation with current loss; the stand volume per acre showed a highly significant negative correlation; and tree vigor showed a significant negative correlation.
>
> "The factor of brush was eliminated and the three remaining factors combined with current loss in a multiple regression which resulted in a highly significant multiple correlation coefficient which showed that about 21 percent of the variability in current loss was explained by these three factors. The factor of reproduction accounted for 43 percent of the explained variation and stand volume for about 35 percent.

> "In the light of other studies, this suggests that a multiple correlation combining past loss, percent of high risk volume, volume per acre, ground cover, and percent growth reduction would explain a high percentage of the variation in future loss."

Based on data from loss and stand cruises already available in the files, Keen (U150) in 1939 devised a method for determining area hazard on an empirical basis. In this he recognized the following ten factors as possibly having some influence on hazard: (1) life zone, (2) elevation, (3) temperature, (4) past losses, (5) growth rate, (6) forest type, (7) site quality, (8) stand volume, (9) stand structure, and (10) fire history. Five of these, numbers 2,4,6,7, and 8 above, were combined on an equal basis by a system of transparent map overlays to arrive at an estimate of future hazard. It was found that the final hazard map derived in this manner required some modification by personal judgment of an entomologist familiar with the area in question. Using this overlay map system, Keen prepared preliminary hazard zonation appraisals in 1939 of 2,580,000 acres of the Klamath subregion (U151) and in 1941 of 1,725,000 acres of the Deschutes subregion in Oregon (U159). These appraisals of hazard zones, while empirical in character, were most useful to timber operators in deciding the priority for cutting of different working circles, taking those of highest beetle hazard first.

Assuming that the percentage of high risk trees in the stand was a good measure of hazard, J.M. Whiteside of the Portland Forest Insect Laboratory made several intensive hazard appraisals of ponderosa pine stands of eastern Oregon, covering the Snow Mountain area of the Ochoco and Malheur National Forests (U325), the Sisters area of the Deschutes National Forest (U324), and the Warm Springs Indian Reservation (U327). Data were taken on past 10 or 12 years of mortality as represented by a count of snags, but hazard maps were prepared only on the basis of the percentage of risk trees in the stand.

In 1942, a new stand cruise was made of some 112 320-acre check plots in Oregon and Washington at which time the green stand was "risk rated" by the California system. By 1947 only 92 of these plots remained uncut and had five years of loss recorded annually on them. This made possible new statistical analyses of the factors most indicative of hazard. Analyses were made by Robert A. Merriam under Keen's guidance in the spring of 1952 (U164). The most significant multiple regression equation for determining expected future ponderosa pine loss in terms of average percent of stand killed per year, was one which integrated the factors of (1) volume of ponderosa pine per acre in M. bd. ft., (2) number of Risk 4 trees per 100 acres, (3) past loss in number of pine snags per 100 acres, and (4) percent of normal growth in last 5 years. The multiple regression equation thus determined was $Y = 0.71 - 0.025x_1 + 0.001x_2 + 0.002x_3 - 0.006x_4$. From this formula an alignment chart was prepared. The standard error of estimate was calculated to be 0.27 percent of the stand. This equation represents the best integration of hazard factors obtained from any of the hazard studies so far conducted.

Special Environmental Hazards

Distrubances of environmental conditions, either man-made or resulting from natural forces, may occur at times which greatly increase the hazards of western pine beetle epidemics within an area. Most important of these are the slash left after logging and clearing, windfalls, and forest fires.

Slash areas.-- Under certain conditions slash creates conditions which are favorable to the build-up of western pine beetle populations which subsequently attack standing green timber. These conditions, however, are so sporadic that generalizations regarding the relation of slash to epidemics are often contradictory and the matter has developed much controversy among entomologists and foresters. One reason for the interest in the relation of slash to epidemics is that slash conditions are largely the result of man's activities and it is possible to regulate cutting operations or dispose of the slash in such a way as to avoid the threat to standing timber.

One of the first workers to stress the entomological danger of slash was Ralph Hopping (49,52), who very definitely

✓ was of the opinion that ponderosa pine slash should be regarded as a potential source of western pine beetle epidemics, particularly where slash included the large dimensions which provided bark areas suitable for brood development of the beetle. This was concurred in by Swaine (123) and represented the Canadian forest entomologists' viewpoint.

The western laboratories of the Division of Forest Insect Investigations made a series of studies in California and Oregon from 1921-1934 to determine whether the western pine beetle actually does breed successfully in slash left from logging and right-of-way cuttings, and how often and under what conditions epidemics occur as a result of these operations.

Person (U225) studied the success of D. brevicomis broods in the slash material left on eleven logging areas and two right-of-way clearings in southern Oregon and California. He found that the ratio of beetles emerging to parent beetles attacking was far less than in infested standing trees. The averages from 1,425 pieces of slash examined showed 15.6 beetles attacking to 19 beetles emerging per square foot of bark. This represented a brood mortality so high that practically no build-up of beetle population in the area was possible and such proved to be the case, as no serious western pine beetle epidemics occurred in the areas which he studied. Person attributed brood failure to the rapid drying out of the slash material and suggested that slash which is scattered out so that it is well exposed to the sun is much less likely to develop beetle populations than slash which is piled so that the larger pieces are shaded.

The slash left from right-of-way clearings where the trees are not promptly utilized was considered to create conditions that were much more favorable to beetle population increases than logging slash, because the logs are usually pulled to one side and are frequently left under shaded conditions. Patterson (99) made a study of this type of slash in southern Oregon from 1920 to 1924, during the construction of a highway across the Greenspring Mountain. He found that D. brevicomis was attracted to the down logs in numbers, but that brood mortality was high. "The increase of beetles developing in the slash was only 64 percent of the beetles making the attack (in reality a decrease in population of 36 percent), whereas there was an increase in adjacent standing timber of 135 percent."

Patterson studied the course of the infestation in zones on either side of the right-of-way for two years preceding and three years following the cutting of this right-of-way slash and concluded that:

> "Bark beetles from the surrounding standing timber are attracted to the slash at the time of attack and a temporary concentration of infestation occurs in the immediate vicinity. Normal distribution of the infestation is resumed within a year.
>
> "The concentration just mentioned and the breeding of the beetles in line slash do not increase or greatly influence infestations in the surrounding forests. The cycle of an infestation continues regardless of the slash."

In studying the effectiveness of different ponderosa pine "line" slash disposal methods, Person (U230) concluded that "the potential from beetles attacking standing trees is so much greater than that from beetles attacking slash, that any effect on the total infestation would be toward a decrease rather than an increase" in western pine beetle population. He recommended that trees along right-of-ways be felled and limbed or felled, limbed, and the brush burned over the trunk to make them even less attractive to western pine beetle.

Beal (U5,U8,U7,U10,U4,U9) studied intensively the entomological aspects of slash on large logging operations in southern Oregon. His results for the most part confirmed those of Person and Patterson. He found that the western pine beetle was not able to reproduce itself rapidly under conditions of logs and slash found in logging operations. While slash was attractive to the beetles it usually failed to produce successful broods. Beal (U8) states: "The inability of this insect to increase rapidly in slash and felled logs should eliminate it from serious consideration as a menace in ponderosa pine slash areas." He gave special attention to the distances from which beetles may be attracted to down logs and concluded that this influence did not extend more than one-half to three-quarters of a mile in the surrounding timber. He found that in the Clover station unit, logging slash had little effect upon the course of the infestation in the adjacent unlogged areas.

In order to clear up the various issues over the entomological aspects of slash disposal, the Division of Forest Insects published a circular in 1927 (23) which summarized previous publications and the investigative work that had been done up to that time. This publication points out the following conditions which concern specifically *D. brevicomis* in ponderosa pine.

> "Usually the first effect of slash was to increase the infestation in standing trees in the vicinity. In every case, however, this increase occurred simultaneously with the attack in the slash, instead of following the emergence of beetles breeding in the slash.
>
> "Since the western pine beetle breeds only in slash material more than 6 inches in diameter, such as cull logs and butts, the present methods of slash disposal can be of little avail in reducing the number of beetles. Neither can the very strong attractive influence of the slash be avoided. The best way, therefore, to avoid injury to neighboring standing trees is to supply continuously a quantity of logs to absorb the beetles and if necessary to reduce through artificial control the total population of beetles on the area."

This same bulletin recognizes that slash is potentially dangerous as a breeding place for aggressive *Ips* infestations.

> "When they (*I. emarginatus*, *I. oregoni* and *I. confusus*) become sufficiently numerous, if there is a shortage of slash, they may kill young trees and the tops and limbs of larger trees. This damage is very sporadic and usually follows the interruption of logging operations in the summer months."

Although there are no reports dealing specifically with the relation of western pine beetle infestations to outbreaks of *Ips* beetles originating in slash, various survey reports record heavy infestations of *D. brevicomis* which have followed widespread topkilling of large trees by *Ips*. In reviewing the records of *Ips confusus*, Miller (200) stated:

> "The more serious of these epidemics (of I. confusus) have been in association with or followed by D. brevicomis which bred up in the green boles of topkilled trees and carried on the momentum of the epidemic for several years after Ips subsided."

Underlying this hazard of western pine beetle epidemics following Ips outbreaks is the susceptibility of topkilled trees. This is shown by the studies of Keen (U122),who found on the Ashland areas that 26.6 percent of the trees topkilled by Ips confusus were attacked by D. brevicomis within one year after topkilling; and by Person (U229), who found on the Cascadel area that 43 percent of the topkilled trees were attacked within two years after topkilling.

The conditions that favor Ips outbreaks resulting from slash conditions seem to be connected with climatic and seasonal conditions at the time when, or soon after, the slash is cut. Interrupted cuttings appear to be specially hazardous during drought periods. Slash cut in the spring or early in the summer has been found to be more productive of Ips outbreaks in standing trees than that cut in the late summer and fall. This was best shown by Buckhorn (U38,U39,U40) in studies of logging areas in eastern Oregon.

Struble (U298,U302) carried out a series of case history studies of individual slash areas, to see if all areas behaved uniformly, and if not, what significant differences could be found. The records which he obtained brought out a number of inconsistencies in the behavior of *Ips* infestations in and around slash concentrations. In some of the areas that were followed *Ips confusus* bred up large populations in fresh green slash during the spring and early summer, and then attacked living trees in the adjacent stands during the late summer and fall. In other areas, however, where *Ips* developed large populations in the green slash, no subsequent attacks occurred in standing trees anywhere near the slash area.

As a general rule, slash concentrations that produce heavy *Ips* populations rarely serve as a breeding ground for the western pine beetle, and do not lead to western pine beetle outbreaks unless they result in a large number of topkilled trees of large diameter. Under such conditions, an increase in western pine beetle populations can be expected.

Windfall areas.-- Windfalls may be regarded as a form of slash created by natural forces. In areas of heavy windfall which occur during the winter in moist soil, many trees are merely pushed over leaving part of the root system in the soil. Such trees may continue to live in this prostrate condition for several years if they are not attacked by insects. Although obviously in a weakened condition, they maintain the moisture in the inner bark so that conditions are favorable to the attack and brood development of bark beetles. In this important respect, most windfall logs differ from those left in logging slash where the trees are cut off at the stump and a rapid change takes place in moisture conditions of the crown and main bole. As a general rule heavy windfall damage has been followed within a season or two by an increase of western pine beetle infestations in the surrounding timber stands.

Windfall damage can be roughly classed according to the amount of down material within the area affected. Some windfalls consist only of scattered weakened trees which are thrown here and there without mass concentrations; other damage results from violent storms which blow down entire masses of trees, sometimes amounting to a relatively high percent of the stand on local areas.

It is where the mass type of windfalls have occurred that severe infestations of the western pine beetle have followed. One such epidemic on the Mendocino National Forest was studied by Miller (86). A violent windstorm which occurred in January 1921 resulted in the blowdown of the following estimated volume of timber on about 20,000 acres:

ponderosa pine	15,000,000 board feet
douglas-fir	8,000,000 board feet
sugar pine	2,000,000 board feet

At the time of the blowdown western pine beetle infestations in the area had been in an endemic condition for a number of years. Developments which followed are described by Miller:

> "With the sudden creation of this great volume of down logs, it was obviously impossible for this limited bark beetle population to supply enough beetles to attack all of this favorable host material in the spring of 1921. It was necessary first that the beetles increase their numbers. This increase developed rapidly during the first season after the windfall, but it occurred almost entirely in the down logs. The degree of infestation in the standing trees that were killed did not increase materially over that of the two seasons preceding. In the spring of 1922 there was no indication from the number of standing infested trees that a potential bark beetle epidemic existed in the region of the windfalls.
>
> "Suddenly during June and July of 1922 the western pine beetle began to attack standing trees in unprecedented numbers. Trees were killed in groups of from 50 to 100, whereas in previous seasons such killings occurred only in single trees or in groups rarely exceeding four or five... The infestation resulting from the attack of this summer generation of beetles increased the annual loss rate from about 25 to more than 200 trees per timbered section.

> "In the fall of 1922 the attacks of the overwintering generation of beetles showed a very pronounced falling off in numbers. The large grouping of attacks disappeared and the winter loss dropped to less than 30 trees per timbered section. In 1923 the seasonal loss declined to a point even lower than that for 1920, the year preceding the windfall.
>
> "Significant features of this epidemic were (1) the absence of engraver beetle outbreaks in ponderosa or sugar pine (although engraver beetles were noted in some of the down logs, they did not appear as a factor in the subsequent killing of standing timber); and (2) the striking absence of any noticeable killing of standing Douglas fir. This species composed a high percent of both the windthrown material and the surviving stand but the insects which bred in the windfalls were incapable of starting aggressive outbreaks."

Keen (U143) reports a local heavy windfall of [which destroyed] about six million board feet of ponderosa and sugar pine near Fort Klamath, Oregon, in 1921. Unlike the Mendocino windfall reported by Miller, this did not produce spectacular bark beetle outbreaks in the surrounding timber, but was followed by only moderate increases in bark beetle losses during the second and third year after the blowdown.

The most extensive bark beetle epidemics connected with windfalls that have yet been recorded occurred in the pine types of Washington, Oregon, and parts of Idaho and California, following a windstorm in April 1931. These are described by Keen (U143):

> "Combining a heavy beetle emergence from the windfalls with conditions of low tree resistance, the year 1932 set a high mark for bark beetle destructiveness in the ponderosa pine stands of Oregon and Washington.

> "Following the blowdown of April 1931 bark beetles attacked and bred in these down trees during the summer of 1931 and emerged in large numbers in the fall. The first heavy loss in standing timber resulted from these fall attacks, which turned out new broods in the early summer of 1932. New attacks were greatly increased during the summer and fall of 1932, even though beetles breeding in the windfalls were no longer a factor. So in this case we have an example of an epidemic once started in windfalls increasing for two seasons in strength and virulence instead of coming to a sudden end.
>
> "In Klickitat county, Washington, where there was a 25 percent loss of timber due to the wind, there developed an additional 15 percent due to bark beetles. On an area of about 200,000 acres in and adjacent to the Ochoco National Forest in central Oregon windfalls were scattered throughout the forest and were followed by a beetle kill of 10 percent of the remaining stand. On the Metolius area of the Deschutes, the loss of timber due to beetles following the blowdown represented 2 percent of the stand. In fact, spotted throughout the pine region in every place where the windstorm had struck, subsequent losses from bark beetles had occurred. The total loss of pine timber in 1932 is estimated at over a billion board feet.
>
> "In a few cases timber operators were foresighted enough to start salvage operations in the windfalls without delay. In cases where the windfalls were removed before June 1, all the infesting beetles were destroyed and the potential epidemic largely averted. These operations not only paid dividends from the salvage of windfalls but prevented the starting of beetle outbreaks.

A description of the infestation conditions that followed this April 1931 windfall in reserve pine stands on cutover lands of the Klamath Indian Reservation is found in a published article by Weaver (131):

> "During the summer of 1931 the top sides of the logs were attacked by the Oregon pine engraver beetle (Ips oregoni) and by the pine flathead (Melanophila gentilis), while the under and shaded sides of the logs were attacked by the western pine beetle (D. brevicomis) and the mountain pine beetle (D. monticolae). While it was apparent that each windfall supported only a light brood of the western or mountain pine beetles, the windfalls themselves were so numerous that in the aggregate they contained a vast horde of insects.
>
> "The unusually heavy precipitation of the winter of 1931-32 was so favorable for tree growth that it was thought that the beetles would make no headway in the standing green trees. However as the summer advanced, large groups of trees in the vicinity of the previous year's windfalls began to fade and die from beetle attacks. Groups of ten to fifteen thrifty, vigorous trees with breast high diameters ranging from 10 to 30 inches were frequently successfully attacked."

A [recent] spectacular outbreak occurred near Bass Lake on the Sierra National Forest in 1945 and was reported by Struble (121,U296). This was also a mass type of windfall, but was limited to about 500 acres. The storm causing the damage occurred in January 1944. During the season of 1944, following the windfall in January, the western pine beetle confined its attacks to the windthrown trees; then, in the mid-summer of 1945 there was a sudden outbreak of the beetles in the surrounding area. Groups of 10 to 30 trees were common. The heaviest kill and the most frequent grouping were found within the blowdown area, but some isolated groups occurred as far as six miles from the center of the blowdown. This epidemic was similar to that of Mendocino and other windfalls of the mass type both in its timing after the windfall and in the absence of any noticeable Ips activity in the attacks on standing trees. (Figure 44).

Figure 44 .-- Infestation of *D. brevicomis* in 1945 resulting from McLeod Flat blowdown of January 1944, Sierra National Forest, California.

No studies have been made of the effects of the light scattered type of windfall upon western pine beetle infestations, although windfalls have occasionally been referred to in survey reports as the source of certain infestations. In comparing effects of this type of windfall with the more destructive mass type, Struble (U296) stated:

> "Almost every year there are localized blowdowns in certain of forested areas. The scattered character of these logs through the woods tends to minimize their importance as breeding places for bark beetles. The facts, however, are that while separate trees do not breed populations sufficient to cause a virulent type of epidemic, they do increase to a certain extent the number of killed trees within the locality of the windfalls and because of this they too must be regarded as menacing to living timber."

(Page 440a follows)

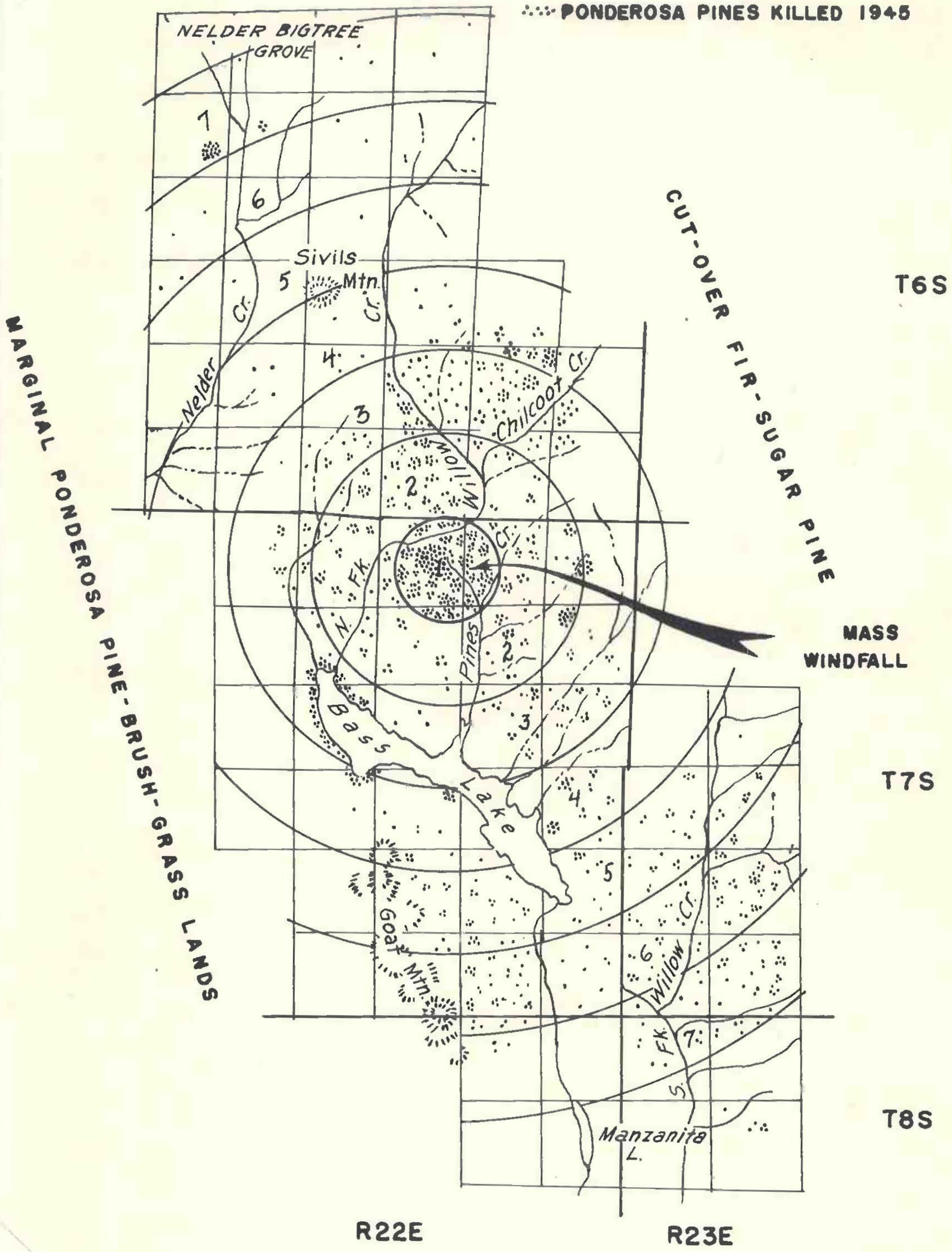

PONDEROSA PINES KILLED 1945
NELDER BIGTREE GROVE
CUT-OVER FIR-SUGAR PINE
MARGINAL PONDEROSA PINE-BRUSH-GRASS LANDS
MASS WINDFALL
Sivils Mtn.
Nelder Cr.
Cr.
Chilcoot Cr.
Willow Cr.
N. Fk.
Pines
Bass Lake
Goat Mtn.
Willow Cr.
S. Fk.
Manzanita L.
1
2
3
4
5
6
7
T6S
T7S
T8S
R22E
R23E

Figure 44 .- Infestation of D. brevicomis in 1945 resulting from McLeod Flat blowdown of January 1944. Sierra National Forest, California.

Forest-fires and bark-beetle relations.— The history of fires in the ponderosa pine region is a very long one. In recent years, since man has taken over the protection of these areas, we have an accurate record of recurrent fires. But for hundreds of years before that the evidence of fire scars imbedded in the tree rings provides a record which shows that mature ponderosa pine stands have [always] been subjected to repeated fires throughout their history. [Chips] Basal sections taken from [the margin of fire scars] fire-scarred trees on more than 100 permanent sample plots scattered throughout eastern Oregon and Washington showed that all plots had experienced repeated fire [in the past] at intervals [averaging about one fire in every] of about 15 to 20 years. One stump section showed a record of 25 fires at approximately 187-year 18.7 ? intervals back to the year 1481 (69). Fires at irregular intervals have been and still are an important phase in the ecology of these stands and cannot be disregarded in considering environmental influences that affect the western pine beetle.

History of investigations.-- Interest in the effect of fires upon bark beetle populations developed very soon after the pine beetle problem became recognized as an important part of forest protection. Hopkins (43) regarded fires as both favorable and unfavorable to *Dendroctonus* beetles, depending upon the area and conditions at the time of the fire. A very live interest in the relationship of fires to bark beetle infestations in ponderosa pine stands began to develop about 1915. This was stimulated in large measure by a school of thought which advocated "light burning." Some lumbermen, stockmen, and others who were familiar with conditions in pine stands before the suppression of forest fires became the chief objective in forest protection argued that fires, when not too severe, had a controlling effect upon bark beetles. These people attributed the increase of infestations in certain areas to the suppression of light fires which burned out the reproduction and underbrush without much damage to the larger trees.

The issue of light burning was brought into the open by two articles by Stewart Edward White (136,137), nationally known author and part owner of the White and Friant Lumber Company. Mr. White stated the case for "light" or "surface" burning quite effectively and was answered in a published article by Chief Forester Graves of the Forest Service.

Other advocates of light burning carried their ideas into practice. For several years prior to 1918 the Red River Lumber Company in northeastern California burned over a considerable acreage of their holdings with controlled fires. Their purpose was to improve ground conditions for early logging, but they also advocated light burning as a measure for protecting mature trees from bark beetle attack. Other less responsible advocates of the theory were prone to start fires surreptitiously whenever they considered conditions to be right, either for selfish ends or in the belief that burning would be for the general good of the country. All of this agitation for light burning ran counter to the efforts of the Forest Service and other forest protection agencies to establish a strong fire exclusion policy in pine stands. Arguments for and against light burning including its entomological aspects became highly controversial and the theory was praised by some and damned by others without much supporting evidence on either side.

The need for factual information on the effects of fires in ponderosa pine stands and their relation to bark beetle epidemics led to a series of studies and experiments by the Forest Service and the Forest Insect Division which extended over the period from 1919 to 1938. Eleven individual burns involving western pine beetle infestations in ponderosa pine type were studied and analyzed in formal reports. In addition data have been collected in connection with annual bark beetle surveys on 10 other burns. These areas are distributed in both eastside and westside pine type from the Cleveland National Forest in southern California to the Coeur d'Alene in Idaho. All types of burns have been represented in the studies - from light ground fires to heavy crown fires. The phases of the problem which have been investigated include (1) the immediate effect of fire upon current beetle population, (2) the relative losses caused by fire and beetles within the burns, (3) the relation of fire injury to beetle attack, and (4) the effect of fires in the ecology of ponderosa pine stands.

A list of the burns which have been studied and for which reports are available is presented in Table 7, page 445a. We find that the studies can be grouped into the following categories:

Controlled burning experiments to test the practicability of light burning and to study both its silvicultural and entomological effects. These are the Snake Lake and Weed Lumber Company burns in California.

Uncontrolled fires causing varying degrees of fire damage in which the reaction of beetle populations within and around the burns were studied. These include the Chinquapin, Mistletoe, and Siskiyou burns (U176,U208), the Northfork burn (U193,U197), the Aspen Lake burn (U216), the Sugar Hill burn (U240,U252), the Parker Mountain burn (U214), and the Tubbs Hill burn (U245).

Uncontrolled burns on which not only the immediate effects of the fire were determined, but extended records over a period of about 20 years were secured showing the long term effects of fire on western pine beetle environment. These are the Northfork and South Ice Cave fires.

Table 2- 7

Studies of Bark-beetle Conditions Following Fires in Ponderosa Pine Type

Name of Burn	Date and Location	Acreage	Type of Burn and Special Conditions	Volume of Beetle-caused Loss Following Fire Compared with Loss for Year Preceding		
				1st Year	2nd Year	3rd Year
			A - Western Pine Beetle Infestations			
Chinquapin	Sept. 1915 Ashland, Ore.	220	Hot ground fire with medium crown injury	+ 475 %	Decrease	Increase
Mistletoe	Oct. 1917 Ashland, Ore.	800	Mixed ground and crown fire with varying degrees of defoliation	+ 1150 %	+ 336 %	+ 122 %
Siskiyou	Aug. 1918 Ashland, Ore.	200	Mixed ground and crown fire with varying degrees of defoliation	+ 1700 %	+ 2880 %	+ 1210 %
Northfork	June 1924 Sierra N.F.	5,460	Mixed ground and crown fire with high percent of defoliated trees	+ 843 %	+ 4680 %	+ 482 %
Aspen Lake	July 1926 Klamath Falls, Ore.	8,000	Mixed ground and crown fire; defoliated trees salvaged within year after fire	Slight increase	Normal	Normal
Sugar Hill	July 1929 Modoc N.F.	5,000	Mostly severe crown fire with about half of stand fire-killed; severe cambium injury in surviving trees	+ 326 %	+ 340 %	+ 49 %
			B - Mountain Pine Beetle Infestations			
Parker Mountain	July 1924 Pinehurst, Ore.	15,000	Mainly a north slope surface fire; severe crown injury occurred only in reproduction thickets	(Heavy increase 1st year after fire due to mountain pine beetle in sugar pine; slight increase in western pine beetle)		
Tubbs Hill	Sept. 1928 Coeur d'Alene, Idaho	30	Mixed ground and crown fire with varying degrees of defoliation	(Increased loss immediately following fire due to attraction of Dendroctonus monticolae, Ips, and D. valens to fire-scorched trees; infestation normal by 3rd year after fire)		
			C - Controlled Burning Operations			
Snake Lake	May 1920 Quincy, Calif.	200	A controlled light burning experiment; burning at night by surface fire	+ 1465 %	+ 915 %	Above normal
Weed Co. Light Burning Project	June-Oct.1920 Bray, Calif.	12,000	Area burned at night in small blocks of not more than 160 acres each	(About 10% increase on burned area as compared to unburned areas, 1st and 2nd years)		
			D - Recovery of Pine Stands From Fire Injury and Beetle Losses Over a Long Period			
South Ice Cave	Aug. 1915 Deschutes N.F.	10,000	Mixed ground and crown fire with varying degrees of crown injury	(22 years after the fire the green volume per acre was about the same on burned as on unburned areas. Fire destroyed young trees in stand but high percent of older trees survived)		

Direct control of beetle populations by fire.-- One of the arguments advanced in the light burning controversy was that fires are Nature's way of keeping bark beetle infestations in check. Mr. White (137) suggested that these insects may harbor in the duff or other ground cover and are destroyed by surface fires; he also advanced the idea that the heat or smoke from fires either killed the beetles in flight or drove them out of the area. Forest entomologists have shown that the western pine beetle does not harbor or hibernate in the duff and spends but a relatively short part of its life in the flight stage, so that the chances of adult beetles being killed by going fires are too small to be of importance. Another theory that has been advanced is that fires destroy the broods of the beetle in infested trees.

However, after the beetles become established in the trees, both adults and broods are protected from heat by the thick insulation of the outer bark which seems to explain the fact that records of mortality of broods in trees infested at the time of the fire are rare. Miller and Patterson (U176) reported six infested trees on the Mistletoe Burn which were exposed to considerable heat at the time of the fire, but in only one case was there any evidence of brood mortality which could be attributed to the fire. In the published summary, Miller and Patterson (92) stated:

> "Fires which are not severe enough to burn the bark from infested trees are of little value in controlling bark-beetle infestations. Fires of moderate severity do not kill bark-beetle broods in infested trees at the time of the fire."

Attraction of bark beetles to burned areas.— In their indirect control effects, forest fires may influence western pine beetle infestations in many different ways. As will be shown later bark beetle populations as a general rule concentrate in fire-injured trees surviving the fire. This indicates that these trees are especially attractive to the beetles, either because the scorching of bark and foliage and heating of the phloem and sapwood set up odors that act as attrahents or because these injuries produce changes in the trees that make them susceptible to bark beetle attack.

Odors emanating from fires.-- The odors from smoke produced by burning resins and foliage when fires burn through pine woods is so obvious to the human olfactory sense that it is only natural to suspect that this may cause attraction of bark beetles to recent burns. However a review of the data from burn studies indicates that the western pine beetle is not attracted to burns until long after the odors emanating at the time of the fire have disappeared. On the Mistletoe, Northfork, and Tubbs Hill burns, it was noted that the main force of the western pine beetle attack came during the season following the fire. Miller (U193) reports an experiment made in connection with the Northfork burn studies in which ponderosa pine trees were scorched by controlled burning in April 1927 so as to produce varying degrees of fire injury. None of these trees were attacked by beetles until late September 1927 after any odors that can be attributed to the immediate effects of the fire had disappeared. D. brevicomis then attacked two of the most heavily defoliated trees which had made no perceptible radial growth during the growing season of May to September following the fire.

It has been found, however, that *D. monticolae* and *D. valens* may be attracted to fire-injured trees very soon after the fire. Show (U281) reported for the Snake Lake burn that "the mountain pine beetle attacked fire-scorched trees soon after the area was burned in May." On the Tubbs Hill burn, Rust (U245) found that a large number of mountain pine beetles were attracted to the burn within six to ten days after the fire. The time interval in these two cases is so short that the odors from the fire or its immediate after-effects could have been an important factor in drawing these insects to the burn.

That other species of cambium-feeding and wood-boring insects are attracted to burns almost immediately is well established, although these secondary species have been treated only incidentally in the recorded burn studies. Certain Buprestids, especially *Melanophila consputa* Lec. and *M. acuminata* D.G. come to burns (78) and attack fire-killed trees in great numbers even while the fire is still in progress, and at times become an annoyance to the fire fighters. This attraction can best be explained by assuming that these species of insects are drawn into the burn by the smoke odors coming from recently scorched bark and cambium.

In the case of the western pine beetle, however, the evidence is fairly conclusive that the beetle is not drawn to burns by odors from any immediate products of the fire, but that it concentrates in burns because of some attraction that sets in some time after the fire has occurred.

Mortality of fire-injured trees due to beetles.— All of the burn studies that have been made agree on one point - the western pine beetle does not select trees that have been immediately fire-killed by the burning of all foliage, charring of the bark, and killing of the entire phloem area. When the beetle comes into burns it selects trees which have survived the fire to the extent that they still have some green phloem and live buds which permit a start of new needle growth after recovery from the first shock of the fire. The studies also agree that there is a direct relation between the amount of crown defoliation from fire and the selection by the western pine beetle of these surviving trees.

Fire-defoliated trees.— The relation of crown injury to beetle attack was first studied on the Mistletoe burn by Miller and Patterson (92). An inventory of surviving trees on this burn according to the amount of crown injury was made soon after the fire and subsequent annual records were maintained for three years following.

Mortality of Fire-Injured Trees on Mistoletoe Burn during the

First Three Years after the Fire

Degree of injury	No. of trees	Died from effects of fire	Attacked and killed by beetles	Surviving three years after fire
I. Uninjured by fire	1,577	-	3.1%	96.9%
II. Light injury, only lower limbs scorched	573	-	16.6%	83.4%
III. Medium injury, more than half of crown scorched	113	-	92.0%	8.0%
IV. Heavy injury, all of crown scorched	57	23%	67.0%	10.0%
V. Fire-killed at time of fire	80	100%	-	-

This first attempt to classify the trees on burns according to the degree of fire injury pointed to scorching of the crowns, or defoliation, as the dominant factor in the relation between fire injury and subsequent attack by bark beetles. On the Northfork burn in 1924 a more critical classification of crown injury according to the percent of defoliation was used on three plots of 100 trees each.

Mortality of Fire-Injured Trees on Sample Plots in Northfork Burn

During First Four Years after Fire

Class of injury	No. of trees	% killed by fire	% killed by beetles	% surviving four years after fire
I. No injury visible	27	-	-	100
II. Less than 25% defoliated	61	-	-	100
III. 25 to 50% defoliated	32	-	13	87
IV. 50 to 75% defoliated	45	-	42	58
V. 75 to 100% defoliated	125	-	87	13
VI. 100% defoliated, bark charred, cambium injured	10	100	-	-

The board-foot volume in each fire injury class and the subsequent insect loss in each as estimated for the entire Northfork burn on the basis of sample strips is shown in Figure 45.

Figure 45.—Mortality of ponderosa pine from fire and bark beetles, Northfork Burn, Sierra National Forest, California. Total volume in each class of fire injury and percent killed by beetles within three years after fire of June 21-24, 1924.

The same classification by percent of crown defoliation used on the Northfork burn was later used on the Sugar Hill burn by Salman and Wohletz (U252) and on the Tubbs Hill burn by Rust (U245). Although the percent of mortality was found to be considerably lighter than on the Mistletoe and Northfork burn, the same relationship was found between percent of defoliation and bark beetle attack.

(Page 452a follows)

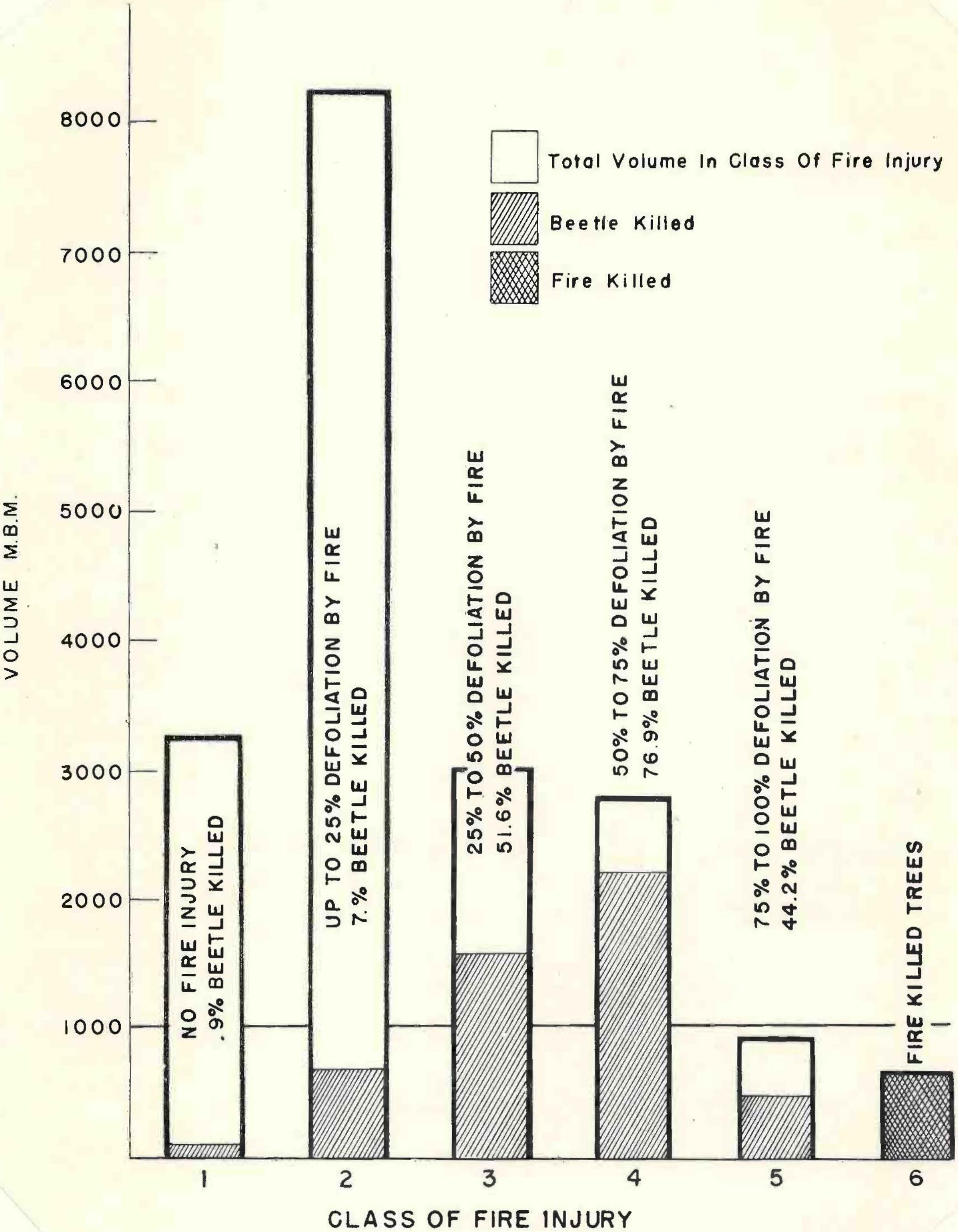


Figure 45.-- Mortality of ponderosa pine from fire and bark beetles; total volume in each class of fire injury, and percent killed by beetles within three years after fire of June 21-24, 1924. Northfork Burn, Sierra National Forest, California.

Mortality of Fire-Injured Trees on the Sugar Hill and Tubbs Hill Burns within Three Years after Fires

Class of injury	Percent of trees killed by bark beetles	
	Sugar Hill burn (One plot of 148 trees)	Tubbs Hill burn (1053 trees in burn)
Less than 25% defoliation	9.0	14.5
25 to 50% defoliation	7.0	14.1
50 to 75% defoliation	23.3	18.7
75 to 100% defoliation	47.7	44.6

The data presented in the above tables from these four burns which have been studied agree in that the percent of defoliation is a fairly reliable index to the expectancy of beetle-caused loss in the trees surviving fire in the ponderosa pine type. Crown injury by defoliation is perhaps the most easily appraised of any of the effects of fire, so that it can readily be applied in surveys of burns for salvage operations.

Cambium-injured trees.— On the Mistletoe and Northfork burns attempts to connect visible basal fire scars with susceptibility to bark beetle attack yielded only negative results. Miller (U197) reported:

> "While it was noted that flathead borers often attacked around the edges of these scars, the records did not indicate any apparent relations between this type of injury and bark-beetle attack. It is altogether possible that a considerable amount of cambium injury (due to overheating) was overlooked in this study since the general run of basal injury in this fire did not burn the outer bark sufficiently to expose the cambium."

On the Sugar Hill fire, Salman and Wohletz (U252) made close examinations for concealed scars in the cambium on all trees included in the plot study. They found that enlargement of former basal scars by the current fire and cambium injury alone in trees which were not defoliated were negative in relation to susceptibility of the trees to bark beetle attack. However, it was reported that: "The susceptibility of trees suffering from cambium injury in addition to foliage injury is markedly greater than that of trees suffering from foliage injury alone."

In a note Salman (111) brought out the following comparison:

Susceptibility of Fire-Defoliated Trees in Relation to Cambium Injury

Percent of defoliation by fire	Percent of trees killed	
	Cambium injury slight	Cambium injury moderate to heavy
0 to 25	8.7	10.0
25 to 50	3.6	13.3
50 to 75	18.2	37.5
75 to 100	19.2	72.2

On the Tubbs Hill burn, Rust (U245) noted that cooking of the cambium around the root cellar was an important factor:

> "Increased injury to the root cellar caused from burning of the extra accumulation of duff on the uphill side of many of the larger pines that escaped severe crown injury was apparent. This severe root cellar injury was found to be a deciding factor in the selection of many fire-injured trees by bark beetles."

In general all studies have shown that the susceptibility of ponderosa pine to beetle attack varies directly with the amount of defoliation caused by fire. This relationship (111) is not greatly changed when cambium injury is also present, except that heavily defoliated trees with moderate to heavy cambium injury are much more susceptible than similar trees with slight cambium injury. In the lightly defoliated trees this differences is much less apparent.

Growth suppression in fire-injured trees.— In looking for an explanation for the susceptibility of fire-injured trees to bark beetle attack, forest entomologists have given a great deal of attention to suppression of growth rate resulting from defoliation and have definitely shown that, for the first few years following the fire, this is the dominant factor in the connection between the fire injury and beetle attack.

Growth suppression during the first four years after the fire was investigated on the Northfork burn by measuring the basal radial growth on all surviving trees on the three sample plots. Miller (U193) found that growth had been greatly suppressed in the more heavily defoliated trees. In many trees no rings were formed during the first two years after the fire.

Percent of defoliation, missing rings, and mortality from bark beetles in trees on sample plots of Northfork burn, 1925-28

Percent of defoliation	Percent that failed to form growth rings 1925-26	Percent killed by bark beetles 1925-28
I. No visible injury	-	-
II. 0 to 25% defoliation	-	-
III. 25 to 50% defoliation	3.1	13.0
IV. 50 to 75% defoliation	15.1	42.0
V. 75 to 100% defoliation	83.2	87.0

This comparison is based entirely on radial growth at the base, but practically all trees which failed to show growth rings in 1925 and 1926 put out new needle growth in the spring of both seasons. Some crown growth was apparent in all trees until they were killed by beetles.

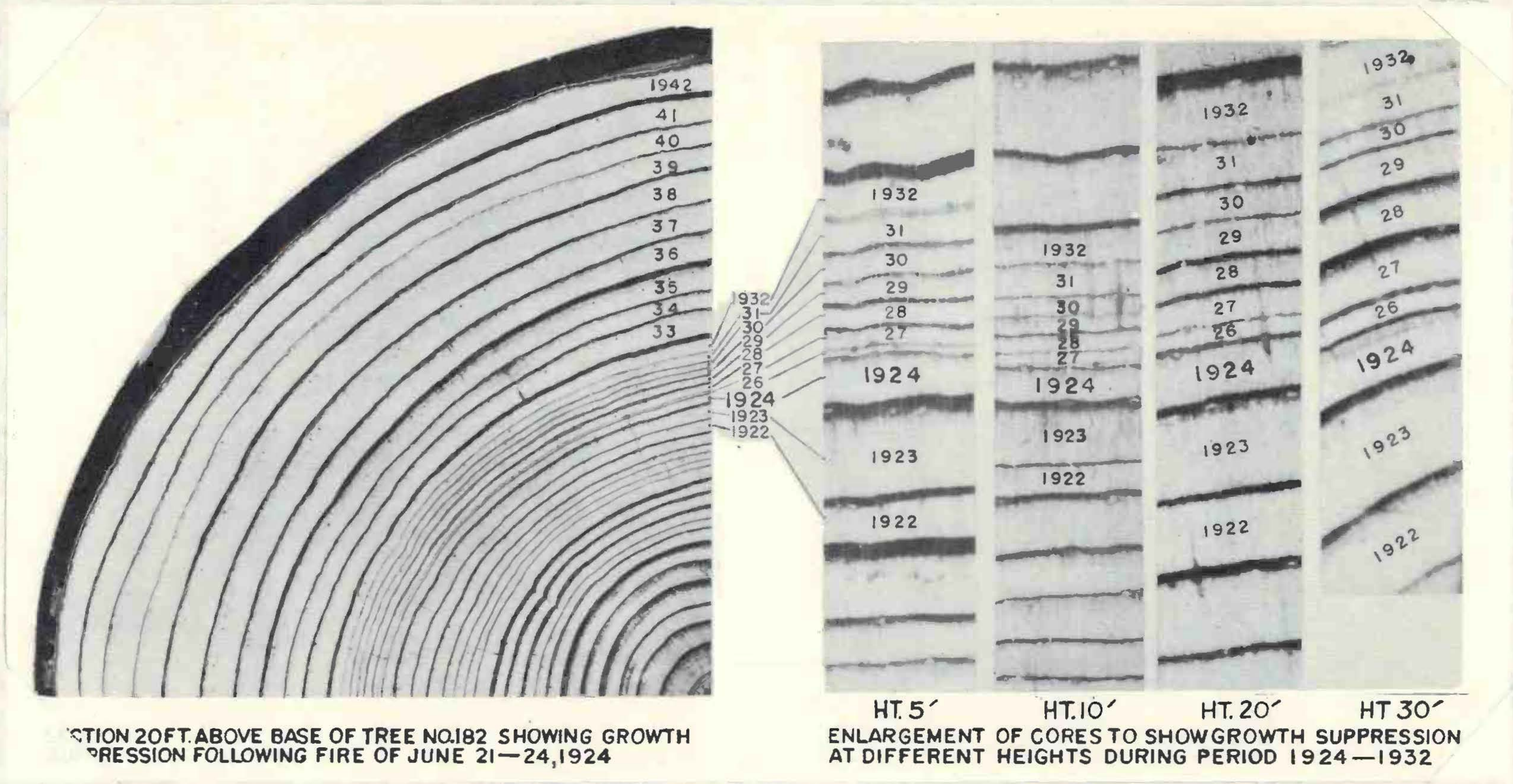
There is some question whether or not those trees which failed to put on basal radial growth the first two years after the fire and survived through 1928 formed some radial growth in the upper bole during these years. This was investigated in the case of two such trees which had survived until 1942. In that season, Miller (U197) felled the trees and measured the radial growth at each 10 foot height interval up the trunks. He found that:

> "There is no significant difference in growth behavior between the base and tops. Missing rings, suppression and recovery of growth rate occurred in the same years at all heights, but suppression of the rings at the base was more pronounced than at the top."

What happened to the tree ring growth of tree No. 182 is shown photographically in Figure 46. This tree was tagged in September 1924, three months after the Northfork fire. It was a dominant in a group of small pole-sized trees on an area of relatively light burn. More than 75 percent of the needles had been burned off (fire injury class V). The tree put on new needles in 1925 and continued to grow until September 1942 when it was cut down and studied for effect of fire injury on the growth rings. Growth suppression during the period 1924-32 was marked, resulting from both fire injury and a series of dry seasons. In the enlargements in Figure 46 it can be seen that no annual ring was formed at any height in 1925, the year following the fire. The 1926 ring is barely perceptible in the lower bole but becomes well marked at the 20 and 30 foot heights. The 1927 ring is well formed at all heights on the bole. After 1927 there was a gradual recovery of growth up to the 1933 season. There followed a 10 year period of greatly accelerated growth. The sudden growth release, eight years after the fire, can be attributed to final recovery from the effects of fire injury and release from the competing pines and vegetation which were killed in the fire.

Figure 46.—Effect of fire injury on radial growth of ponderosa pine, Northfork burn, Sierra National Forest, California, 1924.

(Page 457a follows)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1922
HT. 5′
HT. 10′
HT. 20′
HT 30′
TION 20FT. ABOVE BASE OF TREE NO.182 SHOWING GROWTH
PRESSION FOLLOWING FIRE OF JUNE 21—24,1924
ENLARGEMENT OF CORES TO SHOW GROWTH SUPPRESSION
AT DIFFERENT HEIGHTS DURING PERIOD 1924—1932

Figure 46 .- Effect of fire injury on radial growth of ponderosa pine, Northfork burn, Sierra National Forest, California, 1924

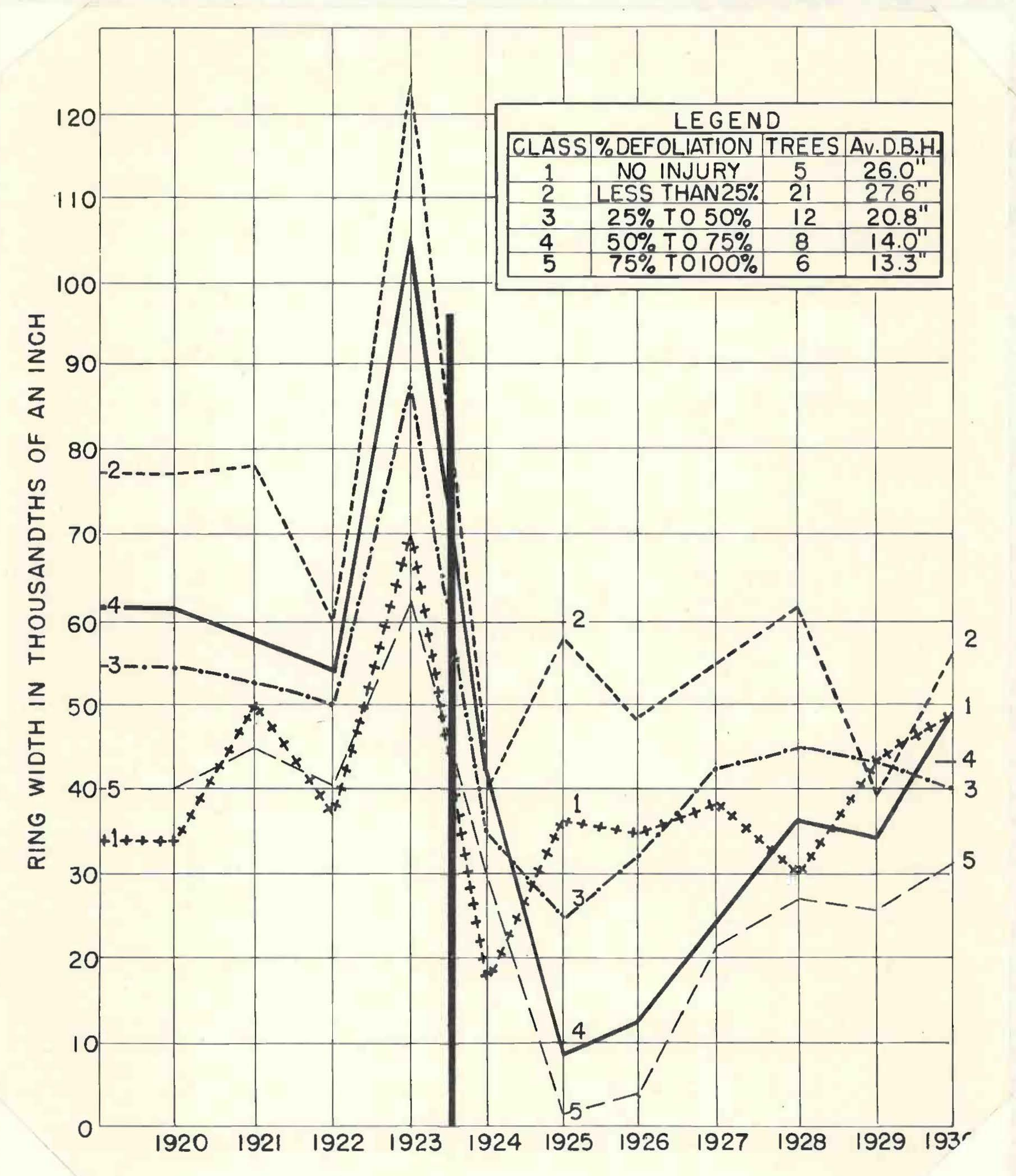
On Plot 2 (Pine Flat), which was lightly burned, 75 trees were found to be surviving with the close of the 1928 season. A comparison of average growth rate for each class of crown injury is shown in Figure 47. This shows that on the average the Class V trees made no recovery during the two growing seasons after the fire, while the less heavily defoliated classes started recovery during the first or second year after the fire. All surviving trees, however, made some recovery in growth the third season following the fire.

Figure 47.--Average annual growth (basal radial increment) by class of fire injury in ponderosa pines surviving on light-burned area. Plot 2 (Pine Flat), Northfork Burn Study, Sierra National Forest, California.

In one plot (Inspector Trail), representing the heaviest type of burn, only 10 out of 100 trees survived through the season of 1927. In 1928 four of these 10 survivors were killed. A comparison of the growth rates of the four beetle-killed and six surviving trees is shown in Figure 48. The surviving trees (5, Class IV; 1, Class V) started growth recovery in 1925, while the beetle-killed trees, which were a slower growing group prior to the fire, made barely visible growth up to the time they were attacked in 1928. All six survivors were still living and making vigorous growth in 1943.

Figure 48.--Comparison of average growth (basal radial increment) of surviving and beetle-killed pines on heavy burn, preceding and following fire. Plot 1 (Inspector Trail), Northfork Burn Study.

(Pages 458a,458b follow)



CLASS	% DEFOLIATION	TREES	Av. D.B.H.
1	NO INJURY	5	26.0"
2	LESS THAN 25%	21	27.6"
3	25% TO 50%	12	20.8"
4	50% TO 75%	8	14.0"
5	75% TO 100%	6	13.3"

Figure 47 .- Average annual growth (basal radial increment) by class of fire injury in ponderosa pines surviving on light burned area. Plot 2 (Pine Flat), Northfork Burn Study, Sierra National Forest, California.

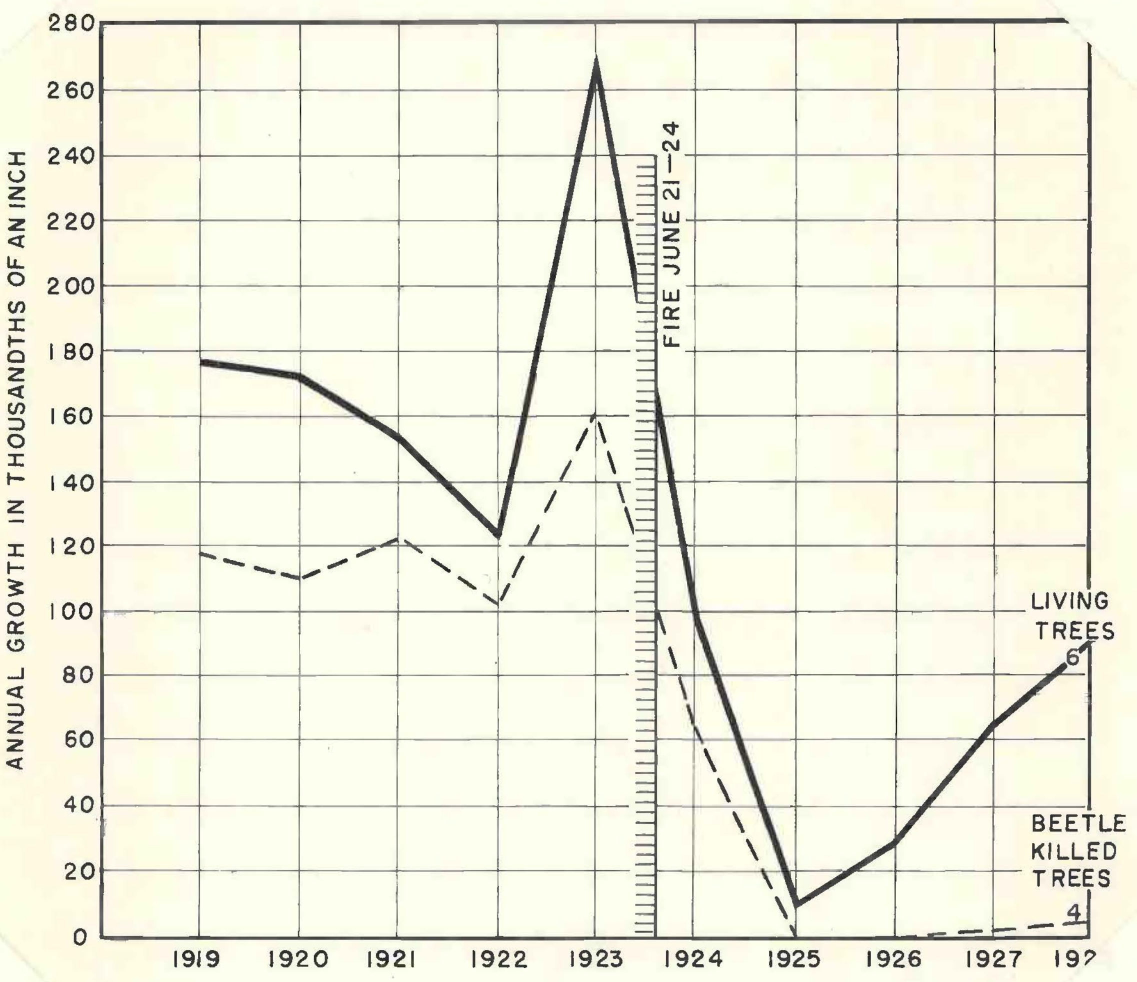


Figure 48 .- Comparison of average growth (basal radial increment) of surviving and beetle-killed pines on heavy burn, preceding and following fire. Plot 1 (Inspector Trail), Northfork Burn Study.

Other studies which have given some attention to radial growth in beetle-killed, fire-injured trees are the Sugar Hill and Tubbs Hill reports, but the data are meager and only indicate that the fire-injured trees killed by beetles were making very little growth recovery.

Growth recovery after fire.— The long-term effects of fire injury upon the growth rate of ponderosa pines were studied by Keen (U161) on the South Ice Cave burn in eastern Oregon. This fire occurred in 1915 and immediately following the Forest Service established three plots of 100 trees each, which were selected on areas representing light, medium, and heavy types of burns. On each of the plots the trees were classified, described, and marked according to the degree of fire injury to the crowns. In 1938, Keen collected and measured basal cores from the surviving trees on the plots. In summarizing the effects of fire injury upon subsequent growth, Keen stated:

> "1. On the average there was no noticeable difference in the effect of the fire according to the side of the tree (on which the heaviest injury occurred).
>
> "2. Growth of small trees was affected slightly more than that of larger trees.
>
> "3. Slow growing trees suffered more than fast growing trees.
>
> "4. Trees less than 50 percent defoliated recovered their normal growth within three years, while trees more than 80 percent defoliated took about nine years to recover normal growth, if they survived.
>
> "5. With an increase in percent of crown defoliated, there was a corresponding increase in the number of trees showing missing rings. One living tree was found which had made no ring growth in the lower bole in the 22 years since the fire."

"6. Reduction in growth rates in the 22-year period following the fire increased slightly with the intensity of the burn, except that slightly burned areas showed somewhat less reduction in growth than normal unburned areas."

A graph comparing average growth rates before and after the Ice Cave fire in each class of fire injury is shown in Figure 49, page ~~459a~~.

Figure 49.--Effect of fire on average growth (basal radial increment) according to degree of fire injury. South Ice Cave Fire, August 1915, Deschutes National Forest, Oregon.

In the supplementary report on the Northfork burn, based on data from 52 surviving trees 19 years after the fire, Miller (U197) found that the trees which had lost 75 to 100 percent of their foliage were the slowest in recovery, but within five years there was a general tendency for trees in all classes of fire injury to level off to their pre-fire growth rates. After this recovery had been accomplished, some surviving trees made phenomenal growth, due to release from competition from adjoining trees which had been killed by fire or insects (Figure 46). This recover in radial growth was accompanied by vigorous growth in the crowns as represented by heavy needle complements, long internodes, and a lush, dark green color of the foliage.

(Page 459a follows)

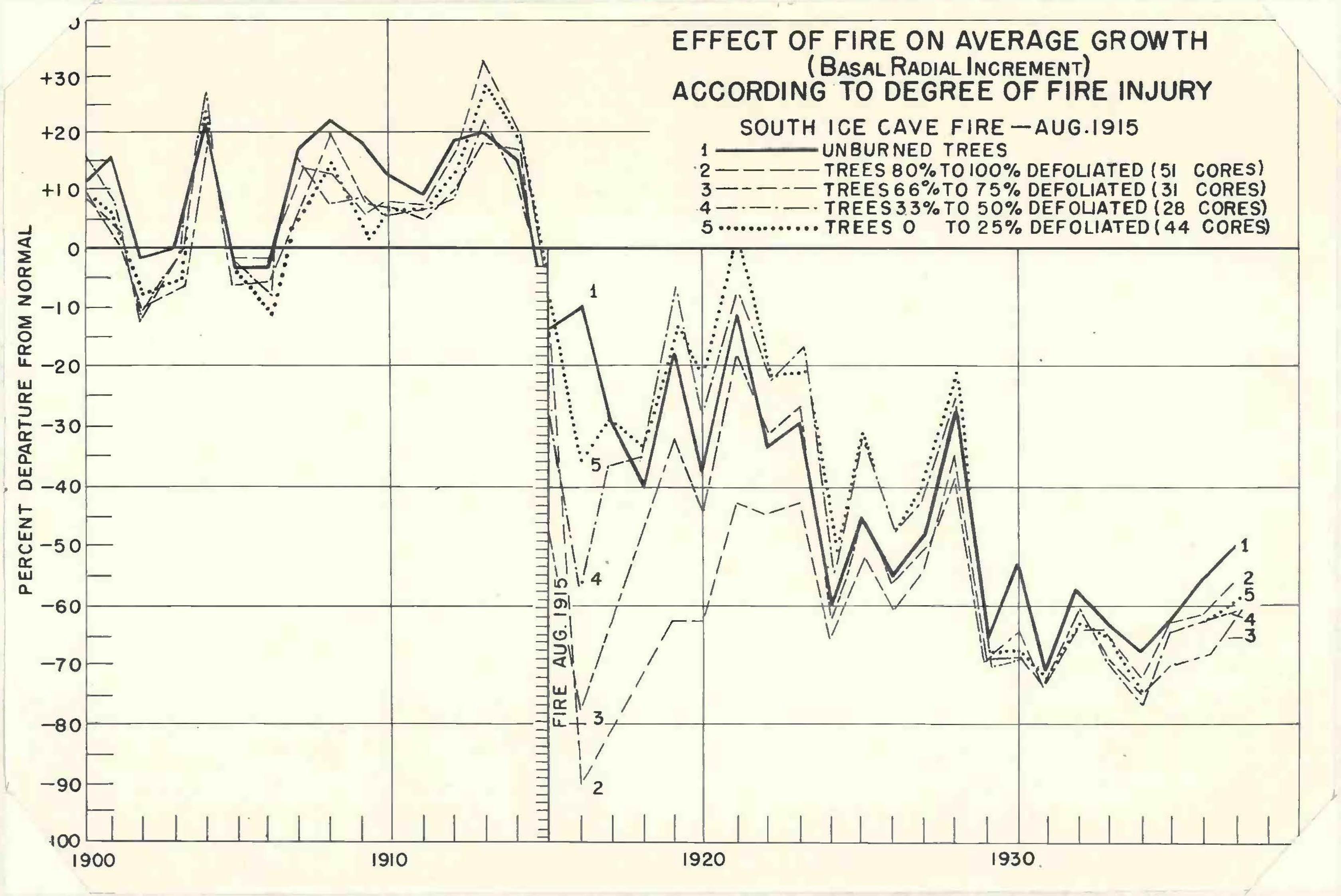


Figure 49 .-Effect of fire on average growth (basal radial increment) according to degree of fire injury. South Ice Cave Fire, August 1915. Deschutes National Forest, Oregon.

In summing up all of the growth studies of fire-injured trees that have been made to date, the evidence points clearly to the conclusion that susceptibility to western pine beetle attack is associated with suppression of growth rate resulting from crown injury and defoliation. This conclusion is supported by the history of western pine beetle concentrations which occur in burns after the suppression of growth has set in. The fact that a few heavily-defoliated trees are sometimes found which escape attack can be accounted for by such factors as climatic influence, the chance distribution of beetle populations, or by the inherent vigor of certain trees to overcome the effects of fire injury and to resist beetle attack.

Success of brood development in fire-injured trees.--This point has direct bearing upon the causes of epidemics that originate in burns. If high brood mortality occurs in fire-injured trees, then epidemic populations cannot be expected regardless of the high concentrations of attack that develop in the burns. However, if the brood development is successful and large populations emerge within the burn, the beetles may spread to adjacent timber. Brood development was investigated on three of the burns that have been studied.

Miller and Patterson (92) reported on the Mistletoe burn:

> "During the season of 1918 it was found that many broods of the western pine beetle in fire-scorched trees were dying in the early larval stages. In trees where this high mortality occurred it was noted that an extremely moist condition of the inner bark was prevalent. Much of the moisture in the sapwood and cambium condensed in the inner bark, resulting in conditions highly unfavorable to the young larvae of the western pine beetle. The term used by cruisers to designate this condition is 'sour sap.'"

A comparison of the number of beetles emerging with the number of parent beetles attacking the same bark areas was used by Miller and Patterson to determine brood success in fire-injured trees as compared with normal trees. Population estimates were arrived at by counting the entrance holes and emergence holes in 272 square feet of bark collected from 28 representative trees on the Mistoletoe burn; similar counts were made from 341 square feet of bark from 76 beetle-killed trees on adjacent unburned areas.

	Fire-injured trees	Normal trees
Square feet of bark analyzed	272	341
Total number of entrance holes	1,372	2,048
Total number of beetles attacking*	3,553	5,294
Total number of beetles emerging**	3,277	22,807
% of increase (emergence over attack)		318%
% of decrease	7.7%	

* Entrance holes x 2.59

**Actual mumber of emergence holes

On the Northfork burn it was found that brood success varied, but not consistently, according to the class of fire injury. Twenty trees were selected in each of the five classes of fire-injured trees recognized on this burn and from these two square feet of bark were collected at each 10 foot height interval. Some increase of beetles was found in all classes except III (25% to 50% of crown defoliated) which showed a decrease of 63 percent in beetles emerging from beetles attacking. No consistent trends could be recognized in the other classes. According to Miller (U193)

> "This would indicate that the beetles built up their numbers in the more severely injured trees which were attacked the first season after the fire; and that the partially defoliated trees in classes III and IV, which composed the bulk of the attack the second season after the fire, were unfavorable to brood development. The high mortality in trees of these classes may account for the decline of the infestation in 1926."

The amount of bark material on which the averages were based for the different classes of fire injury in the Northfork burn is much too limited for reliable population statistics and the results cannot be considered conclusive.

On the Tubbs Hill burn Rust (U245) reported the following:

> "A considerable amount of bark containing overwintering broods of the western pine beetle was taken from fire-scorched trees on the burn in the spring of 1930 and placed in rearing cans for securing reliable data on emergence. An average square foot emergence of 274 beetles was secured from this material showing an average increase of 1,091 percent over beetles attacking, assuming the number of parent beetles per attack equalled two. The emergence per square foot of bark surface for this region secured from a large amount of infested bark surface was found to have a range of 109 to 512, with a general average of 307. The average secured from infested bark from the burn compared very favorably with the average secured from isolated trees over a number of years."

Thus we find that on the three burns where some effort was made to determine the success of broods in fire-injured trees, conditions were unfavorable to brood development on two areas; while on the third brood development seems to have been highly successful. Obviously the conditions which are favorable to brood development in fire-injured trees are highly variable in different burns.

Overall effect of burns upon western pine beetle populations.— Although the beetles do not always multiply successfully in fire-injured trees, the general population in and around burns may be either favorably or unfavorably affected over a period of years by the ecological disturbances due to fires. As a rule western pine beetles have concentrated in the surviving trees on burned areas within a year or two after the fire in such force that it can only be assumed that the beetles came in from outside areas.

On three of the areas that have been studied the volume of beetle-killed timber was measured by surveys prior to the fire and the loss record was maintained within the area of the burn for several years following. The best consecutive records are from the Mistletoe, Siskiyou and Northfork burns.

Increase in beetle-caused loss over year preceding fire in percent of volume

Name of burn	Acreage	1st yr. after fire	2d year after fire	3d year after fire
Mistletoe	800	1150%	336%	122%
Siskiyou	200	1700%	2880%	1210%
Northfork	5,460	843%	4680%	482%

All three of these areas show tremendous increase of infestation during the first and second seasons after the fire as a result of concentrations of beetle population in heavily fire-injured trees.

The Northfork burn study can be considered representative of the behavior of infestations which follow the larger fires in westside ponderosa pine type. On this burn the infestation reached its peak the second year after the fire and even though it made a precipitous drop during the third year, losses were still more than four and a half times as great as the year preceding the fire. Loss records maintained on sample plots indicated that after the third year the infestation dropped below the pre-fire status and remained in this low endemic state over a long period.

Other burns for which the records of infestations following the fire are less complete are:

Chinquapin Burn (220 acres) - losses increased 475 percent the first year after fire; decreased the second year; and increased again the third year.

Snake Lake Light Burning Experiment (200 acres) - losses increased 1465 percent on a tree per section basis the first year and were still 915 percent above the pre-fire level the second year.

Aspen Lake Burn. Beetle-caused losses increased but slightly the first and second year after fire. This was believed to be due to salvage of fire-injured trees in the burn and direct control work in adjacent areas.

Tubbs Hill Burn (30 acres) - heavy concentration of *D. brevicomis* and *I. oregoni* first year after fire; a decline the second year;and return to normal infestations the third year.

Further analyses of these records show that:

1. As a general rule, if the fire occurred in the late spring or early summer, some concentration within the burn developed by late fall of the same year; however, if the fire occurred late in the summer or in the fall, the beetles did not concentrate within the burn until the season following the fire.

2. During the second season following the fire, beetle-caused losses have continued at a high level, increasing over the preceding year in some cases and decreasing in others.

3. The third season following the fire, losses have usually shown a reduction and by the fourth season declined to a point approaching or below the pre-fire level.

4. These concentrations following fires have reached spectacular proportions in some cases. On burns where accurate records have been maintained the annual beetle-caused loss during the first and second years has ranged from 4 to 46 times the amount of annual pre-fire loss on the same area.

5. The intensity of these beetle concentrations and the cycle which they follow has varied in the different burns that have been studied. This can be accounted for by the type of burn, the timing of the fire, and the degree of crown injury in trees which survived the fire.

6. Where salvage of fire-injured trees has been promptly carried out, only slight increases of western pine beetle infestation have occurred within the burn.

In the surrounding areas.— Where the beetles come from which are attracted into burns and where they go to when the large concentrations begin to die down was also one of the first phases of the fire-beetle relationship to be investigated. This interest was at first stimulated by the "light burning" controversy which raised the question whether or not the beetle populations that build up in burns are a threat to adjacent timber.

On the Mistletoe burn study, this question was given a great deal of attention. Prior to this fire the area of the burn and the adjacent pine type of the upper Rogue River Valley had been covered by an annual 100 percent loss cruise which measured the volume and mapped the distribution of all beetle-killed trees. Following the fire, which occurred in the late fall of 1917, these loss cruises were continued through 1918, 1919, and 1920. In order to show the distances to which the influence of the fire extended, the entire area of the pine type was laid out in zones one mile wide extending to a distance of six miles from the borders of the burn. The annual losses from 1917 to 1920 were computed and mapped separately in each of these zones. The results as summarized by Miller and Patterson (92) indicate that the effect of the burn upon the surrounding infestation could be detected for a distance of about three miles.

> "Records thus obtained show that for the general area surrounding the burn there was a slight tendency toward increase of infestation during the season of 1918 (the year following the fire), but at the same time, zones within 3 miles of the burn registered a perceptible decrease. During 1919, however, when the volume of infestation within the burn decreased 74 percent, the first zone immediately adjoining showed an increase of nearly 60 percent, while in all zones beyond this there was a very marked decrease.
>
> "From this evidence it would appear that the natural tendency of the infestation was to increase in 1918 and decrease in 1919. These natural tendencies were disturbed, however,by the attractiveness to the beetles of the fire-injured trees in 1918,which caused many beetles to leave the first three surrounding zones and concentrate in the burn.In 1919,as the attraction of fire-injured trees had subsided,some of the beetle population which had concentrated in the burn attacked trees in the area immediately adjoining, causing a perceptible increase locally,although all other zones registered a decrease."

It was pointed out in the conclusion, however, that the increase in 1919 in the zone immediately surrounding the burn, although perceptible, did not develop into a serious epidemic. What occurred was a local interruption of the infestation cycle, and normal trends were restored within three years after the fire.

The Northfork burn study has supplied data to show that the influence of a burn upon adjacent timber is not always perceptible. In this study the cycle of infestation from 1919 to 1926 within the area of the 5,400 acre fire was compared with that in the adjoining Cascadel check area of 1,880 acres. This comparison shown by Figure 50 is discussed by Miller (U193):

> "The outstanding point brought out by this comparison is that the cycle, both preceding and after the fire, was essentially the same in both areas. They differ mainly in the relative quantity of the losses during the seasons of 1924, 1925, and 1926. The severe drought of 1924 resulted in a great increase of beetle losses throughout the Sierra pine belt which is reflected in the record for the Cascadel area. This increase reached its peak in 1925 and a pronounced drop occurred in 1926 in both areas. On the burn, however, the increase in 1925 was boosted far beyond what would have occurred normally as a result of the drought alone, but the decrease in 1926 was much greater in proportion than that on the Cascadel area."

Figure 50 .--Comparison of pine volume killed annually by bark beetles on burned area (5460 acres) and on adjoining check area (1880 acres), Northfork Burn, Sierra National Forest, California, 1919-1926.

(Page 468a follows)

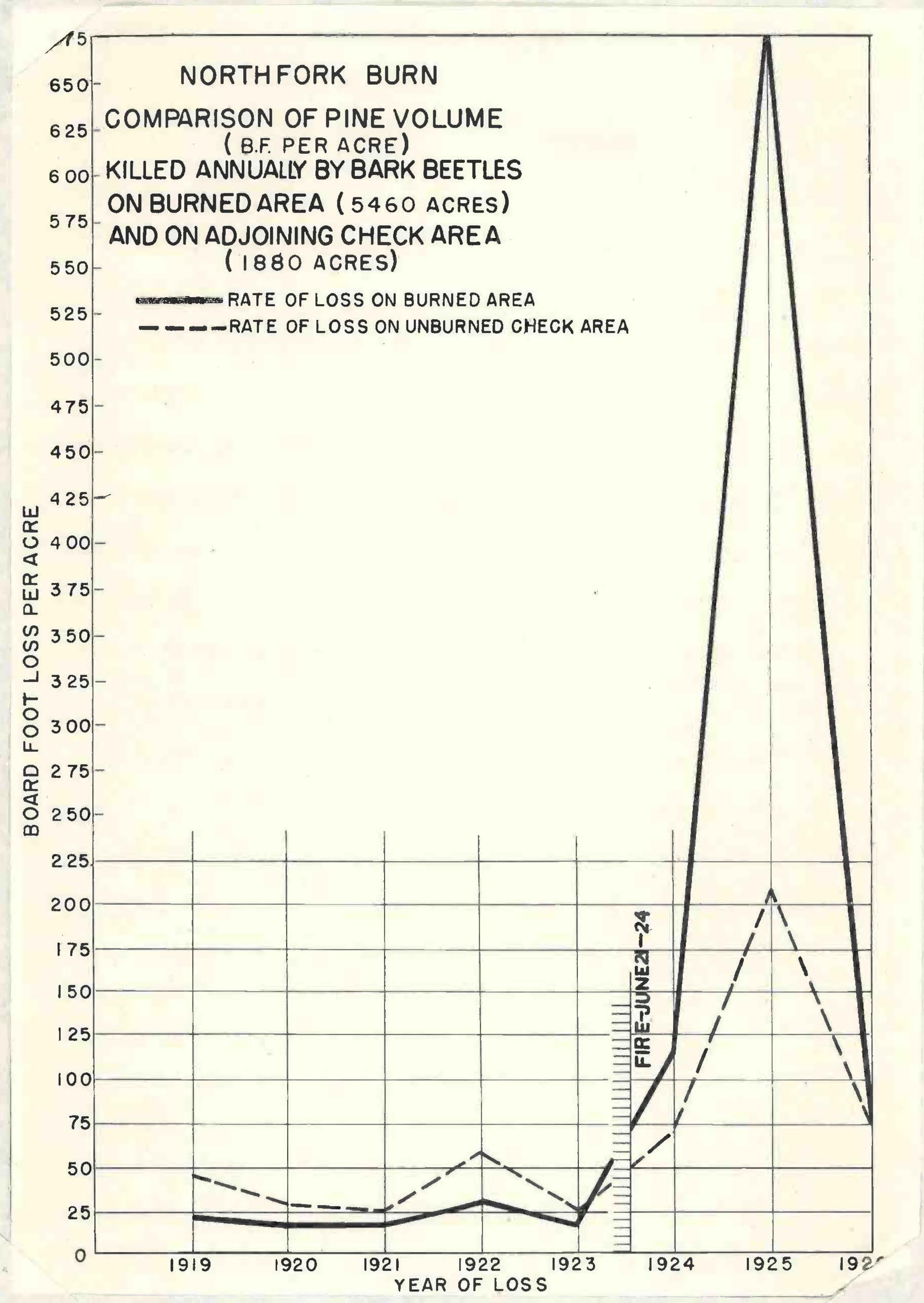


Figure 50 .- Comparison of pine volume killed annually by bark beetles on burned area (5460 acres) and on adjoining check area (1880 acres), Northfork Burn, Sierra National Forest, California, 1919 - 1926.

Although these recorded studies do not indicate that serious infestations spread out of burns into adjoining areas, data from survey and other sources indicate that they do in some cases. One of these reports is found in the 1930 survey report on the Cleveland National Forest by K.A. Salman. Referring to the Coulter pine type of the Palomar district, he states:

> "In 1928 a fire burned out a portion of the stand in Dyche Valley and evidently scorched some of the timber, providing material in which it was possible for the western pine beetle to breed. The beetles emerging from this material apparently spread to unscorched timber outside of the fire area and have continued their intensive attack until at the present time an area of approximately three-fourths of a section has suffered a loss of 65 percent of the stand."

A similar development in Coulter pine type was reported by J.M. Miller in the 1941 survey report for the Cleveland. An Ips-western pine beetle outbreak in the Julian district was explained as follows:

> "This infestation apparently originated around the eastern border of the 1938 burn where it was localized in the fall of 1939. In the fall of 1940 large groups were noted in the area west of Julian which had been relatively free of infestation previously. New groups were also found springing up in the Pine Hills unit to the north, which are also part of the spread from the original center around the burn."

Aside from the Coulter pine type in southern California, several burns have been encountered in the westside pine type of the Sierras from which western pine beetle infestations were believed to have spread into adjoining timber. One of these was the Power Line burn in the southern part of the Yosemite National Park. G.R. Struble reported upon the conditions around this burn in 1943:

> "Groups of ponderosa pines killed by the western pine beetle were evident, particularly along the Wawona road from Chinquapin to the Valley and in the vicinity of Big Meadows. Activity is centered in the vicinity of Big Meadows burn which occurred in October 1941. In the burned area and adjacent to the burn, hundreds of recently faded trees were observed."

In these reports the greatest spread of infestation occurred the second and third years after the fire and was found to extend from the borders of the burn to areas six miles distant. Other fires for which the survey data indicate a spread of serious infestations are the San Joaquin canyon fire on the Sierra National Forest in 1939; and more recently the Black Rock fire of 1943. On the other hand, survey records can be cited for burns from which no spread of infestation could be detected and these cases apparently represent the majority of the burns that have come under observation.

From the available evidence, the spread of infestations from burns to adjacent timber which occurs at times is subject to special conditions. Timing of the fire according to season, brood success in fire-injured trees, susceptibility of trees in the unburned areas, climatic conditions, and the natural upward trend of the infestations can be suggested as possible factors which influence the potentialities of infestations becoming aggressive in the surrounding timber. However, this phase is one that has been given little study and much more information is needed before definite conclusions can be drawn.

Effect of burns upon western pine beetle infestations over long periods.— Although the immediate effect of fire of moderate intensity in ponderosa pine stands is to set up conditions favorable to western pine beetle populations, it does not hold that these conditions persist long after the fire. Changes in the ecology of pine stands may develop in the lighter types of burns which are quite unfavorable to continuing infestations. This was one of the contentions of the "light burning" school of thought.

After the first effects of a fire have subsided we find that within a period of three to five years most of the susceptible fire-injured trees have been killed, the stand of larger trees has been thinned, much of the competition of the older trees with the understory of brush and reproduction has been reduced, and the surviving trees are making vigorous growth. (Figure 46). All studies that have been made of the ecology of the western pine beetle indicate that such conditions reduce the hazard of bark beetle attack.

Some foresters have considered the use of controlled fires in ponderosa pine stands as a silvicultural agent for reducing both the fire and beetle hazards. This theory was most recently advocated by Weaver (132) as a result of his 17 years of observations in the pine region of the Pacific slope. His main argument that total fire exclusion in mature pine stands resulted in a heavy understory of reproduction and brush was stated as follows: "It is believed that the dense, stagnating stands of reproduction that have developed on vast areas have aggravated the beetle losses tremendously as a result of their competition with the larger trees for the limited soil moisture."

This adverse effect on mature stands of dense understory competition for available moisture, as reflected in heavy beetle damage, and the great reduction in beetle damage in areas where fires have removed the competing understory has been repeatedly observed by forest insect survey men in the ponderosa pine stands of the interior type where soil moisture is such a critical factor. In fact, it has become axiomatic to expect heavy beetle damage in stands choked by stagnating brush and reproduction, and light losses in burned stands, after the first three to five year period, where this competition has been removed.

Keen compared beetle damage on two adjacent areas of the Happy Camp district of the Modoc National Forest, California in 1926, one of which had been burned seven years before, by a fire which had removed the understory but had made no reduction in the board foot volume of the reserve stand. Pine beetle damage was extreme throughout the unburned stands, but light on this burned area. Two plots where the reserve volumes were essentially the same compared as follows:

Plots and condition	Acreage 100% cruised	Estimated Beetle loss per section Trees killed 1925	Summer 1926
Unburned			
Heavy understory of brush and reproduction	320 acres	200	250
Burned in July 1919			
Ground with no brush or reproduction	80 acres	40	20

The long-term effect of fire upon conditions that relate to bark beetle hazards in pine stands were studied on the South Ice Cave Fire of the Deschutes National Forest, Oregon. These studies by forest officers extended over a period of 22 years from 1915 to 1937. Keen (U161) summarized conclusions from a 1937 examination of the plots. He states:

> "Analysis of stand conditions on the 1915 burn and in the surrounding areas indicated a larger number of trees per acre off the burn, but a larger volume per acre on the burn, in trees of larger diameter and volume per tree. Stand structure analysis showed a dearth of younger age classes on the burn and with a higher percentage of trees in beetle-susceptible classes than in neighboring areas.
>
> "From a snag count and check of current 1937 pine beetle damage, a somewhat heavier loss of timber was noted outside the burn than inside, but the variability between plots was too large to permit conclusive data on this point.

Thus in general, the long term effect of fire is to lessen western pine beetle ~~bark beetle~~ damage rather than increase it.

(No text for page 475)

SECTION V

WESTERN PINE BEETLE SURVEYS

HISTORICAL

Bark beetle surveys are designed to determine what species of beetles are causing timber losses, where the infestations are located, and how much timber is being destroyed. This information provides the basis for determining how important infestations are and what should be done about them. Both research and control work are guided by the basic information obtained by surveys which determine the amount of loss, obtain other vital data, and provide the basis for interpretation of conditions in areas infested by western pine beetle and associated insects.

Dr. A.D. Hopkins'(41) western trip in 1899 appears to be the first undertaking that can be classed as a survey to determine the importance of this beetle. This was followed by Webb's work (133) in Idaho in 1904-05. These preliminary surveys did not attempt any measurements of losses, but they did establish the importance of the western pine beetle as an actual and potential threat to pine resources. Some years later (about 1910) timber owning agencies, both private and public, began to recognize the importance of the problem and became interested in knowing just how much timber they were losing. It was these agencies that initiated the first quantitative surveys. At the same time the Bureau of Entomology began the measurement of beetle-caused losses on selected areas to serve both its research and control activities. Gradually these surveys were expanded into an annual program which now covers with varying degrees of intensity most of the western pine region.

The methods used in conducting western pine beetle surveys have varied widely. The most elementary method has been merely to view the area to form an impression of the extent and character of the losses. This was the method obviously used by Hopkins and other pioneer investigators. From this elementary approach, methods have developed in which the techniques used by foresters in arriving at timber estimates have been adapted to beetle-killed timber. Of the many survey projects that can be included in the history of western pine beetle investigations, we will review only the early projects which led to the present day region-wide forest insect survey program.

Klamath River Survey of 1911

The first record of an intensive survey for the purpose of measuring the amount of beetle-killed timber was the "Little Humbug Creek" survey on the Klamath National Forest just west of the town of Yreka, California. Because of the apparent depletion of ponderosa pine stands in the Klamath River watershed, Forest Assistant A.H. Hodgson (U95) made a survey of five sections, the purpose of which was to "gather accurate data regarding the topography, condition of timber, general history of the area, and an estimate of green and dead timber on representative sections where yellow pine, sugar pine, and Douglas fir are infested and being damaged by insects."

Because this seems to be the first undertaking of its kind the technique that was used is of interest. Hodgson ran a 10 percent strip through each forty.

> "The crew consisted of three men, a compassman who ran the line, sketched topography, and made an ocular estimate of the timber; and two tally men. The dead timber was classified as *white tops*, *red tops*, *black tops*, *standing snags*, and *down snags*. The compassman also located for each entire section the white tops or trees freshly attacked by the western pine beetle."

Thus Hodgson was probably the first to prepare a "spotter's" map by fixing the location of each infested tree by means of a "spot" or tiny circle on the survey map.

The total depletion of pine measured on these sections in 1911 ran into rather formidable figures, averaging about 40 to 50 percent of the stand on the most heavily infested sections. (82). On the less heavily infested [lighter] sections the accumulated loss was from 10 to 20 percent. In a letter to the Forest Supervisor commenting upon Hodgson's report, J.M. Miller (U167), who worked on the entomological phases of this survey, estimated that "the total loss figures for dead yellow pine represented the accumulated loss of about 30 years."

In the fall of 1911 other surveys were made by the Yreka station of the Bureau of Entomology in the Moffat Creek watershed and other areas of the Klamath National Forest in California, mainly to obtain estimates for control recommendations. These were mainly reconnaissance surveys supplemented by the cruising of sample sections using the same methods of mapping as were used by Hodgson. These first quantitative surveys seem to have set the pattern of methods for the more extensive programs which followed.

The Klamath-Lake Counties Surveys, 1911-1920

Private timber owning agencies around Klamath Falls, Oregon, were among the first to become interested in bark beetle control. About 1910 the Klamath-Lake Counties Forest Protective Association under the leadership of Jackson F. Kimball began to inquire into the problem and in 1911 initiated preliminary bark beetle surveys in some of their holdings. In order to cooperate, the Bureau of Entomology started a field station at Klamath Falls, which furnished technical assistance in spotting for the first control project in the Parker's station tract in 1912. For a period of some years following, the Association maintained an annual surveillance of its holdings to locate areas where the bark beetles were active; and from 1914 to 1919 W.E. Glendenning, Agent for the Bureau, assisted on this enterprise.

Control Surveys by the Forest Service, 1912

The first control projects of the Forest Service in the California region were started on the Klamath, Sierra, and Trinity National Forests in 1912. In connection with this work, a number of reconnaissance surveys were made to determine the need for further control work in addition to the spotting on the actual control operations. The more important preliminary surveys were made by Forest Examiner Ralph Hopping. In 1913 the Regional Forester adopted the procedure of requiring an annual report upon current insect conditions for each national forest. This called for a report from each district ranger based upon general observations or upon more factual surveys where these were considered to be necessary. This procedure by the protection force has been adhered to up to the present time, but has been supplemented by a considerable amount of more intensive survey work by the forest insect field laboratories of the Bureau of Entomology.

Rogue River Surveys by the Ashland Station, 1915-24

Beginning in 1915 the Ashland station of the Bureau of Entomology began a series of quantitative surveys to obtain data for research purposes. These were designed to serve as a basis for studies of the biology and epidemiology of the western pine beetle, and also to study the accuracy of survey methods. This project has already been described under epidemiology in Section III, pages 293-296, and the more pertinent survey reports have been referenced under Miller (U170, U173) and Patterson (U212). The method of survey used was to view units of the area topographically and to count and map the insect-killed trees. "Certain portions of each watershed were also cruised intensively and all trees examined and marked. An estimate was then made for each area, using the results of the extensive viewing as a basis and interpreting them by the results obtained on these sections which were intensively cruised and all trees examined." The project area was concentrated in units of the Rogue River watershed near Ashland where loss records were maintained for the entire period of the study. However, from 1916 to 1918, inclusive, the surveys included parts of the Applegate and Klamath River watersheds, making a total area of 350,000 acres.

The California Survey of 1917

Up to this year bark beetle surveys seem to have been prompted mainly by interest in special areas where unexpected or spectacular infestations had aroused concern of the timber owners and most of them were made as the first step in the initiation of control projects. The first comprehensive survey to acquire an overall picture and analysis of conditions within a general subregion seems to have been the cooperative undertaking which was termed the California Survey of 1917.

This survey was undertaken primarily as the result of an agitation among a group of private lumber companies in California who were disturbed over the bark beetle situation of that period. Some individuals advanced the theory that infestations were increasing because of the policy of total fire suppression which was then becoming established on both federal and private timber lands. The agitation was brought to a head in January 1917 when three of the larger lumber companies, in addition to the California Forest Protective Association, petitioned the Secretary of Agriculture to "make an immediate investigation of the extent and seriousness of the loss caused by bark beetles."

This 1917 survey was organized under the direction of the Bureau of Entomology. The Forest Service contributed the time of three of its technical men, and the Bureau of Entomology detailed four men from the Ashland station. Private owners, the Forest Service, and the National Park Service contributed funds to finance the field expense of examinations on their own lands. The area covered included the western flank of the Sierra Nevada Mountains from the Rubicon River as far south as the South Fork of the Tule River. The entire project was completed during the summer of 1917. The accomplishments and recommendations of the survey were presented in a series of reports by Miller, Hopping, and Jaenicke (U168).

Was it a report or a series?

As stated in this report, the methods used "consisted of extensive cruising, supplemented by sample plots from time to time which furnish the necessary data for the proper interpretation and significance of the counts obtained in the extensive cruises." Usually the Forest Service and Bureau men worked in field parties of two men each, or singly with the assistance of local representatives of the cooperating agencies.

The summarized results of the 1917 survey included the following:

Period of survey	June-October 1917
Total acreage of pine type examined	1,682,000
Stand of pine timber represented (ponderosa, Jeffrey and sugar pine)	19½ billion board feet
Total pine loss estimated	25,570,000 board feet
Cost of field work, salaries and expenses	$3,200.

Southern Oregon-Northern California Project Surveys, 1921-24

Concern over rapidly increasing infestations in the Klamath Basin reached a climax in 1920 and brought about the initiation of a large cooperative control project in 1921. The project as finally put into effect included 1¼ million acres of pine timber land made up of extensive holdings of the Klamath Forest Protective Association, the Indian Service, and the Forest Service. As a basis for control plans, it was necessary to bring together all available information on losses and stand conditions. This summarization and analysis of conditions was made by A.J. Jaenicke (U97) during May 1921 by going to the land-owning agencies for their file information on current conditions and by carrying on only enough reconnaissance work to interpret this information. In the fall of 1921 a detailed loss survey was made and the project area was divided into control units. During the next two years the project, under Keen's direction, was organized into a series of reporting units and areas on which records were maintained up to and including the 1932 season. The survey program for the project originally included 34 check sections, nearly all of which contained 640 acres, supplemented by roadstrips and topographic estimates. Aside from obtaining the overall picture of conditions over the entire area of over one million acres, the purpose of this continuing annual survey was to determine results of the control work, the need for further work, and to provide a basis for planning action programs. The first summarized reports of these surveys were prepared by Keen (U135).

The main cooperative phases of the project were closed down in 1924, but loss surveys were continued annually by the Bureau of Entomology as a basis both for research projects and for control recommendations. A long series of annual survey reports have been prepared by Keen (U146).

The Regional Detection Surveys

After 1931 the Bureau of Entomology and Plant Quarantine maintained annual loss surveys within the ponderosa pine region on a regional basis, using the Forest Service regions, such as Region 5 (California), Region 6 (Oregon and Washington), or Region ~~7~~ 1 (Idaho and Montana) as the base. Within the region, national forests or other federal holdings, such as national parks and Indian reservations, and the large bodies of privately owned land, served as reporting areas.

The general plan that has been followed, in all regions, consists of two phases: (1) preliminary scouting and reports by field offices of federal land agencies, and (2) quantitative surveys by the Bureau of Entomology and Plant Quarantine alone or in cooperation with federal land agencies or private timber owners.

District Rangers on all national forests report unusual forest insect outbreaks to the Forest Supervisor who in turn reports to the Office of Timber Management of the Regional Forester. These reports are usually of an observational nature, calling attention to any conditions that seem to warrant further attention. The information is summarized by the Regional Forester who consults with the local Forest Insect Laboratory for final recommendations and action. Control work is carried out by the land managing agency under technical guidance of the forest entomologists.

For many years the entire ponderosa pine type was not covered by these regional surveys. The bark beetle problem was not considered of sufficient importance in some areas to warrant detailed surveys; and even if warranted, funds and personnel were not available to maintain a complete regional coverage. Consequently, the annual survey program was concentrated where the beetle problem was of most significance. This included commercial pine stands that were being depleted and recreational tracts where the maintenance of tree cover was considered to be important. Since passage of the Forest Pest Control Act in 1947, the forest insect survey program has been enlarged to cover all forest areas, at least with aerial observations to detect outbreaks. The expansion of coverage has necessitated cutting down on the intensity of sampling. More general information is now being obtained on more areas, with less detailed sampling of any area except those where control work seems desirable. On such areas an intensive appraisal survey is made.

Research Objectives of the Regional Surveys

In addition to obtaining an annual record of the intensity and trends of bark beetle damage, so as to be prepared to control outbreaks, the regional survey has often included research objectives. In many cases, information of outstanding value has come out of the survey program as a valuable by-product.

Salman (U249) defined two research objectives of the California regional survey as: -

> "1. To attempt to correlate intensity and trends of forest insect infestations with physical factors of climate, soil, altitude, topography, the biotic factors, etc.
>
> "2. To obtain information concerning effects on a stand of heavy infestations, particularly as regards changes in the susceptibility of the stand."

In Oregon and Washington, the study of tree susceptibility (67,70), climatic cycles as indicated by tree rings (68), and the rate of falling of ponderosa pine snags (64) are examples of the studies which the regional survey program made possible.

Regional Reports

As the data have accumulated currently from the regional surveys, occasional summarizing reports have been issued in mimeographed form for each region to give the overall picture of forest insect infestations and the interpretation of conditions. The reports that have been issued up to 1952 include the following series:

California surveys

Results and recommendations, forest insect survey, Region 5. Season of 1931. J.M. Miller and K.A. Salman.

Regional survey of forest insect conditions in the California region, 1931-36. K.A. Salman.

Forest insect conditions in the California region for the 1937 season. Forest Insect Laboratory, Berkeley, California. (1938)

California forest insect conditions 1946. Division of Forestry in cooperation with Forest Insect Laboratory.

Forest insect conditions in California 1949. California Division of Forestry in cooperation with Forest Insect Laboratory, U.S. Bur. of Ent. & P.Q.

Forest insect conditions in California 1950-51. California Division of Forestry in cooperation with Forest Insect Laboratory, U.S. Bur. Ent. & P.Q. Sacramento January 1951

Forest insect conditions in California in 1951. California Division of Forestry in cooperation with U.S. Bur. of Ent. and P.Q. Sacramento, California, January 1952.

Oregon and Washington surveys

Annual report of forest insect conditions in Oregon and Washington for 1933. Forest Insect Laboratory, Portland, Oregon, May 1, 1934.

Forest insect conditions in Oregon and Washington, 1933-38. Forest Insect Laboratory, Portland, Oregon, July 1, 1939.

Forest insect conditions in Oregon and Washington, 1938-1942. Forest Insect Laboratory, Portland, Oregon, July, 1946.

Forest insect detection surveys in Oregon and Washington Season of 1950. Oregon State Board of Forestry and Bur. of Ent. and P.Q. September 30, 1950.

Forest insect detection surveys in Oregon and Washington Season of 1951. Oregon State Board of Forestry and Bur. of Ent. and P.Q. Forest Insect Laboratory, Portland, Oregon, November 15, 1951.

Forest Insect Hazard Surveys

The results of studies carried on in connection with bark beetle surveys in the eastside pine type from 1931-35 began to point the way toward the recognition of susceptibility to bark beetle infestations in certain areas and types. This led to the development of still another type of bark beetle survey, the object of which was not only to measure current losses, but to appraise the stands according to potential losses that are liable to occur in the near future (see hazard zonation, pp. 419-427). Such surveys have immediate practical value for logging operators by pointing out areas of greatest hazard where much of the potential loss can be avoided by immediate or early logging.

The first survey of this character was undertaken on the Lassen National Forest in 1936. This was mainly a tryout of the methods and ideas that had been developed up to that time. In this trial survey, the Eagle Lake tract of some 23,000 acres was zoned according to five degrees of hazard. The report prepared by Salman and Johnson (U272) was distributed to private and federal owners of the tract with recommendations for treatment of the area.

This preliminary work on hazard rating met with the interest and support of the pine operators, and in the fall of 1937 the same type of survey was organized and initiated to include the entire eastside type of northeastern California. This program required four seasons and eventually covered 2¼ million acres. As units of the area were completed each season, progress reports were prepared and issued to the operators concerned. The final summarizing report for the entire project was prepared under the joint authorship of Miller, Salman, and Johnson (93).

Lacking funds to conduct similar hazard surveys in eastern Oregon, Keen in 1939 analyzed existing office data from timber surveys and annual insect loss surveys and prepared preliminary hazard appraisals of the Klamath subregion of 2,580,000 acres (U151) and in 1941 of the Deschutes subregion of 1,725,000 acres(U159).

Later hazard surveys were made by J.M. Whiteside of the Portland Laboratory of three critical areas in eastern Oregon, i.e. the Sisters area of the Deschutes National Forest, the Snow Mountain area of the Ochoco National and Malheur National Forests, and the Warm Springs Indian Reservation. These hazard appraisals were based solely on the percentage of risk trees in the stand.

Subsequently in 1951, M.M. Furniss (U59) made a new hazard appraisal of the 95,000 acres of old-growth ponderosa pine in the eastern Lassen National Forest of California, using the hazard regression formula developed by Keen and Merriam.

Bark Beetle Survey Manuals

The need for a bark beetle survey handbook giving the essential information used in conducting field projects was recognized soon after the first control work was undertaken. The first instructions on survey methods appeared in a manual by Ralph Hopping (48) issued by the Forest Service of District 5. This manual was fairly specific and detailed in its instructions for conducting control work, but survey methods were treated only under "spotting," i.e. marking trees to be treated on control projects. In the appendix Hopping listed the points that should be taken into account and reported upon in "forest insect reconnaissance," a term used for pre-control surveys. The greater part of the manual was taken up with information on the more important tree-killing insects, the causes of infestation, and special instructions and forms used in control work.

A short article by Miller in the Timberman in June 1925 (84) discussed the purposes of forest insect surveys and the methods used up to that date.

Two manuals by Keen (58,60),prepared in 1926 and 1927, included detailed instructions dealing with the organization and methods of making bark beetle surveys, as well as organizing and carrying out control projects. The second manual, which was a revision of the first, included a complete discussion of the approach to the problem of obtaining adequate information on current infestations and loss estimates. The instructions dealing with sample plot work were detailed. The costs of survey and the accuracy that can be expected were presented in tabulated form. This manual included a number of useful charts and reference tables, including (1) number of trees and acres ordinarily spotted per day by a three-man spotting crew, (2) chart showing open seasons for bark beetle control by species and regions, (3) table of measurements for construction of a Biltmore scale, (4) table giving total bark surface for each diameter and height of tree, (5) table giving comparative accuracy and costs of different types of surveys, and (6) sample forms used in mapping, marking, and tabulating infested trees and the reporting forms used in different types of surveys.

In 1933 a forest insect handbook was prepared by F.P. Keen and A.J. Jaenicke for use in the North Pacific Region (126). This handbook, which was designed to apply to all of the more important forest insects of the region, discussed surveys both for research purposes and for control. Detailed instructions were given for the operation of a three-man survey crew in spotting, mapping, marking, and recording infested trees. Instructions were also given for the preparation of annual reports required of forest officers. Instructions were given for the selection, setting up, and measurement of losses on sample plots, and useful tables were included for determining the period of attack of both infested and recently abandoned trees.

In the California region a field manual of bark beetle survey methods was prepared by P.C. Johnson (53) in 1935, mainly for use in the development of the regional survey program. This manual contained instructions for both intensive and extensive types of surveys and outlined the organization, procedures, and equipment used in the establishment and measuring of losses on permanent sample plots. The methods of marking plot boundaries and the strip cruise lines on regional survey plots with metal markers, originally devised by Salman, were described in detail. This manual is the only one that provides for the setting up of plots on cutover lands; it is also the only one giving instructions for analysis of infestations by bark surface measurements, otherwise known as "stem analyses." The appendix contains tables for use in (1) correcting compass alignment, (2) symbols to designate forest type, (3) definitions of site index, (4) definitions and illustrations of the Dunning and Keen tree classes, and (5) descriptions of infestation types. The correction factors for estimating the total seasonal loss cruised at any date is shown by curves for the Modoc and Lassen Forests and for the westside Sierra pine region. Sample forms for records and reports and instructions for their use are included.

A handbook of instructions for the establishment and measuring of [large] 320-acre plots in mature virgin pine stands of Oregon and Washington was prepared by W.J. Buckhorn in 1944 (13). Its chief purpose was "to facilitate the training of personnel and improve the quality of the work" in the use of standardized methods of plot surveying. The organization of the three-man crew and duties of its members was treated in detail. The manual contains keys for the identification of beetle-killed trees according to the year in which they were attacked; instructions for the use of the compass, Biltmore stick, and other equipment; and the sample forms used for recording and reporting of data. It also includes a set of original volume tables for both green and insect-killed ponderosa pine on different sites as developed from height curves from sample plot measurements in eastern Oregon. Buckhorn describes the method of risk rating trees by the use of "penalty scores" for individual tree health characters as developed by Keen as a supplement to his bark beetle susceptibility classification. This manual also describes the Keen tree classification slide rule and its use in checking the classification of border-line trees.

Other references to forest insect survey methods are contained in the textbook "Forest Insects" by Doane, Van Dyke, Chamberlin, and Burke (30 ,pp.39-44) and in U.S. Dept. Agr. Misc. Publ. [Bul.] 273,"Insect Enemies of Western Forests" by F.P. Keen (74, pp.227-233). In the latter, forest insect surveys are grouped according to their intensity and purpose and are classed as (1) "detection of bark beetle outbreaks" by the field officers of land-owning agencies, and (2) "extensive bark beetle surveys" to determine the intensity, size, and character of the infestation and whether or not control operations are justified. Under (2) both topographic and sample strip methods are described.

SURVEY METHODS

For the most part, bark beetle survey methods have been evolved out of practical experience with forest mensuration techniques as applied to beetle-killed timber with such modifications as are needed to provide for the collection of a considerable amount of entomological data. In actual practice, methods are often modified to suit forest types, the character of the infestation, seasonal conditions, and the particular purposes for which the information is to be used. We find that survey methods have been critically studied at times by forest entomologists to evaluate their efficiency, relative costs, and the possibilities for their improvement. The phases that have been considered in these studies include (1) the units by which the quantity of infestation is measured, (2) the methods of area coverage, and (3) the correction factors used in formulating estimates.

The Units of Loss Measurements

The entomological purposes of bark beetle surveys usually require that the amount of the infestation be expressed in some quantitative way. This can be done by using units of measurements which will express either the number of trees or volume of timber killed or the quantity of beetle population in relation to the time period covered and size of area involved.

The Number of Infested Trees

The simplest way of expressing the amount of infestation within an area is to count the number of infested and recently killed trees. The advantage of a simple tree count is the ease with which it can be used in visual surveys. Were all trees of uniform size within an area this unit would serve as a fairly satisfactory basis for computing both loss volume and the amount of infested bark surface representing beetle population. But in practically all western pine beetle infestations, infested trees vary greatly in size within the same area and between areas. Consequently, the number of trees does not give a true quantitative picture unless their size and volume is known and totaled.

Regardless of quantitative accuracy, the number of trees killed annually per section is a commonly used unit on all reconnaissance surveys. An experienced estimator can often arrive at a rough estimate of the average size and volume of beetle-killed trees within an area and thus translate his visual counts into estimates of timber volume lost.

The infested tree, regardless of size, must be regarded as a biological unit in that the individual tree is the center of attraction for a number of attacking beetles and the localized breeding place for a seasonal generation. In actual control work the individual tree is a unit which cannot be disregarded in work plans since each tree must be spotted, felled, burned, or otherwise disposed of. Consequently, it is important to know the actual number of infested trees within an area as well as their total volume and this item has always been an important element in survey data.

Board-Foot Volume

The considerations calling for board-foot volume in the expression of beetle-caused losses have led to the almost universal practice of measuring the diameter and height of each infested tree in bark beetle control surveys. This may be done for all trees within the area as on a control project or on selected sample plots only.

Loss in Relation to Acreage

Board feet per acre is a derived unit which has been frequently used as an expression of intensity of loss in relation to acreage of timber land infested. It is a measure commonly used by foresters and easily visualized by them. It is also easily computed, once the loss volume and acreage are known. It can be accepted as a fairly good comparison of the intensity of loss between areas where stand conditions are comparable. The disadvantage of this unit is that it does not give a true comparison of infestation intensity when the stands are not equal, i.e. of different types or volume, or where large areas of non-timbered or non-pine type forest land are involved. For instance the loss of 100 board feet per acre in a stand of 5,000 board feet of pine per acre is of much higher intensity than the same loss in a stand of 25,000 board feet of pine per acre. In the first case it would be considered an epidemic infestation, while in the heavy stand it would be rated only as an endemic infestation.

Loss in Relation to Stand Volume

For comparative purposes the percentage of stand volume killed, derived by dividing the volume of loss by the stand volume, gives the best index to the intensity of losses. Percentages are a common expression of relationship and are therefore easily visualized by most people. In this case, percent of stand killed gives a ready comparison with growth percent and also indicates the rapidity with which stands are being depleted. While this unit is probably the most useful of any in showing the seriousness and progress of bark beetle infestations as related to the stands in which they are working, its use is limited by the lack of available or reliable stand estimates in many areas. Another disadvantage is that where heavy losses or selective cuttings are depleting the stand, the base on which the percentage is computed is changing and has to be revised from year to year. This also prevents the addition of yearly percentage figures in order to arrive at the total percent of stand killed over a decade or other period of time.

Infested Bark Surface and Unit Trees

The units of measurements so far listed have been derived from forest mensuration practices and have been largely taken over in bark beetle surveys with little modification. However, forest entomologists have devoted some effort to finding a unit of measurement that would serve as a more accurate measure of the quantity of beetle population. On the average the infested bark surface of a given tree has a direct relation to the number of beetles which attack and emerge and it is therefore an indicator of beetle population. If a unit tree represents a fixed area of bark surface, it can also be used as a measure of beetle population.

In 1915 Keen (U129) carried out a series of surveys on the Ashland areas in which he used infested bark surface and a hypothetical "unit tree" based upon a constant area of infested bark as a unit representing beetle populations. In order to facilitate the computation of bark surface area from survey records, Keen prepared a table giving the total bark surface for each tree of a given diameter and height. Where more than one species of beetle occurred in the same tree, the amount of bark surface occupied by each was apportioned by measurements or estimates of infested lengths occupied by each species. Non-infested bark areas were also computed. These bark areas were then totalled by species and these totals divided up into unit trees composed of a fixed number of square feet of bark surface.

The idea of using a standard unit tree was first proposed in the supplement to a survey report on the Applegate watershed in 1916 (U124). The specifications suggested in this report were for a unit tree 24 inches DBH, 80 feet in height, and covered by 50,000 square inches of infested bark. Later, in the final summary of quantitative studies on the Lamb's Mine area (U129), a somewhat smaller unit tree was used with the following specifications: DBH, 20 inches; height, 80 feet; infested bark surface, 200 square feet. Following these specifications, the 1915 overwintering infestation on the Lamb's Mine area was totalled and expressed as follows:

1915. Overwintering infestation, Lamb's Mine Unit, Rogue River area.

Actual number of infested trees	217
Total area of infested bark surface	45,514 sq.ft.
Total number of unit trees (200 sq.ft.ea.)	227.57
Infestation by species:	
Dendroctonus brevicomis	188.60 unit trees
Other bark beetles	8.90 unit trees
Unknown	30.07 unit trees
Total	227.57 unit trees

The idea behind a standard unit tree in bark beetle surveys was to find a measurable unit which would compensate for the great variation in the size of actual infested trees and lack of uniformity in the infestation occupying the infested bark surface. Although the idea of the "unit tree" is basically sound, it has never come into general use because it means more conversion of basic data into an arbitrary standard not recognized by anyone outside of this special field.

Methods of Area Coverage

The first step in making a bark beetle survey is the decision as to the manner in which the area is to be covered in order that all or a part of the infested trees can either be seen or examined and measured. The methods of area coverage which have been used to date have been designated as (1) topographic surveys,(2) sample plots, (3) road strip surveys, and (4) aerial surveys.

Topographic Surveys

(also designated as topographic reconnaissance)

Keen gives the following description of this method:

> "The estimator, equipped with binoculars and a topographic map of the area, 'gridirons' the country by traveling along ridges or open valleys or wherever an unobstructed view may be had of most of the timbered area. At selected points along the route, the opposite slopes or areas visible and not more than two miles away are viewed either with the naked eye or with the binoculars,and the red, sorrel or faded trees counted. These are then spotted upon the map within the area which has been viewed,either by dots or numbers, to indicate the number of trees that have been counted. All the country that can be viewed is covered in this manner.

> "To determine what percentage of the trees have probably thus been counted, a check plot which has previously been viewed, should be intensively cruised and the ratio between actually infested trees and the number viewed on this area determined. Experience has shown that in general through the western yellow pine type the number of discolored trees counted by the viewing method on slopes not more than two miles away will have to be multiplied by two to arrive at the approximate number of infested, dying or dead trees on the ground."

Factors used in topographic surveys.— Topographic surveys were first used as a basis for quantitative estimates by Keen (U124) on a survey of the Applegate area. Later Keen (U125) defined the factors used in correcting estimates for topographic surveys and clarified procedure in their use.

> "*The use of the factors.*
>
> 1. Count *total* fading, sorrel and red standing trees without regard to year of their death.
> 2. Multiply (trees counted) by factor for type of country seen, light, and proximity of area.
>
> *The factors.*

When every tree can be seen	1.0
All of country seen, near view, good light	1.5
Broken country nearby, or moderately broken rolling country at distance; good light	2.0
Broken country, deep canyons at a considerable distance, poor light	2.5
Broken country, deep canyons at a considerable distance, dark days	3.0
Very rough country, large areas hidden from view	3.5

> 3. Multiply by personal factor (must be determined for the individual)

Overestimate factors	.75 to 1.00
Consistent factors	1.00
Underestimate factors	1.00 to 1.50

> 4. Then multiply by ratio of old and new loss as determined by actual cruise of infested standing trees on a section or several sections of timber."

In 1933 DeLeon (U50) used topographic methods for a permanent system of detection surveys on the Sequoia National Park. He initiated several refinements in the method that were designed to improve the accuracy of the data and to make it possible to follow losses in the same areas year after year. Permanent observation points were established from which counts were to be repeated each season, panchromatic photographs were taken which brought out the faded and red trees, and a plane table and alidade were used in mapping the position of each tree. These innovations are quite adaptable to the steep topography of the southern Sierras where there are good lookout points from which to view the pine type. Unfortunately, due to change in personnel, this system was dropped after the second year so that this refinement of method was not given an adequate test.

In general practice where the country does not view well, as in flat or rolling terrain, general viewing of the timber is combined with, or entirely replaced by, counting of beetle-killed trees along roads, trails, or selected traverse lines, or on strategically located check plots. This amounts to a strip survey or plot sampling the general area and when enough trees are examined and measured, a very good basis for survey estimates is obtained.

With the advent of the automobile and development of roads in forest areas it was found that a preliminary estimate of the infestations could be obtained very readily by counting recently killed trees along the roadway while travelling by car. This method has gradually been developed and measurements added so as to yield estimates of considerable accuracy. This will be discussed later under road strips.

Check Plots

In the early surveys, topographic estimates were supplemented by the intensive cruising of a few sample plots or "check plots," on each area. On these plots all beetle-killed and infested trees were located, examined, measured, marked, and mapped. In addition, entomological data were collected relating to the insect species responsible for the death of the trees, the stage of brood development, and conditions of the broods. While such plots were originally referred to as "sample plots," they were not samples in a statistical sense, so should more properly be called "check plots." The tendency was to locate them, not where average conditions prevailed, but rather where the heaviest loss occurred. Once the actual loss and trends were known on one or more check plots, even though they represented the maximum loss conditions, the estimator could visually compare these plot centers with other sections in the area and judge whether the losses were heavier or lighter than the ones he had measured. Thus the check plots served not as samples, but as yardsticks for estimating the whole.

Keen (60) says that "the sample plots (check plot) may be anywhere from 1 to 640 acres or more in size, but either a half or a full section is selected as being large enough to give a fair sample of conditions in the vicinity." The first extensive use of check plots was in connection with the southern Oregon-northern California pine beetle control project on which a series of 60 or more full section, 640 acre, plots were used to check on control results and the need for further work. These large plots were also used extensively by the Indian Service on the Klamath Indian Reservation until 1937.

After 1931, a large series of half-section check plots, 40 chains wide by 80 chains long, containing 320 acres, were cruised annually in [both] northeastern California, eastern Oregon, and Washington, as a basis for determining infestation trends and for other studies. Less emphasis was placed on making general area or regional loss estimates from them, but they also served this purpose. These plots were considered to be large enough to include most of the variable conditions found in a fairly large sample of the pine type and hence good indicators of the general rise and fall of epidemics in the vicinity. They also represented fairly large areas of forest land on which changing forest conditions could be followed over a period of time. Another reason for adopting the half-section plot as a convenient working unit was that under ordinary conditions it was possible for a three-man crew to carry out, in one day, all of the details of measuring the annual loss. Thus the time schedule of surveys could be planned on the basis of one day for each plot. These check plots were recognized as being too few in number to give a reliable sample of the total loss in the pine type, but they did provide the maximum information that could be obtained with the time and manpower available.

Sample Plots

With the advance in statistical methods came a desire to put surveys on a sound sampling basis and to get away from estimates based on check plots and the judgment of individual estimators. A sample plot should represent a small part of the entire infestation area and enough samples should be taken so that the average conditions can be determined with a measurable degree of accuracy.

In 1938 a field study of sampling procedure was started by R.C. Hall (U80) in the Burney area of the Shasta National Forest, California, to determine the number, size, and shape of plots which would give an adequate sampling of the whole area of about 250,000 acres. The loss records and maps of the half-section regional survey plots in northeastern California made it possible to analyze probable results by breaking these down into smaller units of varying shapes and sizes. These plots were divided into smaller units of 5, 10, 20, 40, 80, and 160 acres and the average annual board foot loss per acre was computed for each plot for each year over a six-year period. The relative efficiency was then determined by measuring the relative variability between plots of different sizes and shapes. Among the results found were:

> "The range in loss on the smaller plots is relatively much greater for a single year than it is for the average of six years. (Some 20-acre plots showed no loss at all on certain years.)

> "Theoretically the most efficient plot size of those tested proved to be the five-acre unit. However, the gains in efficiency of the fives over the tens and the tens over the twenties were so slight that they can hardly be considered practical.
>
> "Although there is considerable variation in the 20-acre plots, the combining of these smaller plots into large units even up to 160 acres has not materially reduced the variation and it has been found that there would still be considerable variation in 320-acre plots which are side by side.
>
> "The shape of a plot appears to have some effect on its efficiency, although only slightly so. It was found that the long, narrow plot was generally more efficient than a square one."

In 1939, a series of forty 20-acre plots were established by Hall (U80) in the Burney area and for a number of years losses were measured on these annually. Hall computed the sampling error for 37 of these plots for the four year period 1938 to 1941 inclusive and found it varied from 35 to 48 percent. He states: "A sampling error of about 40 percent for the whole unit of about 250,000 acres seems very high and may not be much better than a guess on the part of an experienced observer." Thus unless the coverage with small plots is more intensive than the 0.3 percent used on this area, the small plots do not offer any real advantage over half-section plots for survey purposes. In both cases the plot data needs to be supplemented by general observations. It is also evident that the amount of travel time between plots when a series of well distributed small plots is used, makes their coverage more costly than a cruise of the same amount of acreage in one or two large plots. Another disadvantage of the small plot is the greater possibility of error in deciding whether trees along the boundaries are in or out of the plot,because their total perimeter is much greater than that for the same amount of acreage enclosed in one large plot.

In 1951 a conference on survey methods was held at Fort Collins, Colorado, by the Forest Insect Investigation Division men engaged in surveys (U86). It was agreed that all intensive surveys should be so designed that a valid estimate of sampling error would be possible. It was also agreed that completely random sampling, while theoretically desirable, was not practical for most of the western survey problems. The maximum acceptable error to be tolerated for small units was set at 25 percent at the 68 percent level. This would require a different amount of cruising depending upon the size of the unit sampled, as is shown in the following table:

Size of unit to be sampled (acres)	Western pine beetle surveys			
	Percent of sample needed		Number of plots	
	10 acre plots	320 acre plots	10 acre	320 acre
1,000	28.0%	50.1%	28	1.5
2,000	16.3	33.6	32	2.1
5,000	7.2	16.7	36	2.6
10,000	3.7	9.3	37	2.9
15,000	2.5	6.4	37.5	3.
20,000	1.9	4.9	38	3.

Later in the spring of 1951, R.G. Hall with the assistance of J.W. Bongberg and M.M. Furniss of the Berkeley Forest Insect Laboratory and Dale C. Prentice of the Western Pine Association carried out a field study at Black's Mountain Experimental Forest to test the effect of size and shape of plots on efficiency in the making of an appraisal survey of 18,000 acres of virgin eastside pine. The most efficient of all methods tested proved to be the half-acre circular plot established at five chain intervals along a compass line, with a sample coverage of 2½ percent. The field work was carried out by four one-man crews using compass and pacing and running two lines through each section at 40 chain intervals. The cost was found to be about 3 cents per acre. A survey of this type using systematic sampling techniques is most appropriate for appraisal surveys of limited areas where estimates are needed for control. Such intensity of coverage is not feasible for annual loss surveys on a statewide or regional basis.

Road Strips

The recent development of road systems throughout most of the national forests, many of which traverse valuable timber stands, opened up the possibilities for using road strips to a much greater extent than formerly in bark beetle loss surveys. The almost universal use of auto transportation in forest work and the ease with which surveys can be made by using cars or pickups to automatically measure distance traversed by speedometer instead of the slow, tedious pacing of section lines on foot gives a special appeal to the use of the road strip method.

In many of the first surveys, trails, wagon roads, or highways passing through the timber type were used as located lines along which the infested trees were counted as a basis for loss estimates. In some surveys the trees along these road strips were examined and measured for a fixed distance of several chains on either side. When a survey of this character is run for a distance of a mile or so the road strip becomes for all practical purposes, an elongated plot. Considerable study has recently been given to improvement of the accuracy of the method, with the expectation of using it to replace half-section plots in virgin stands which must be abandoned as they are cutover in the advance of logging operations.

Hall (U80) adopted the roadstrip method for the Hat Creek sampling study as a check against the results obtained by the sample plot method. The system used was a strip ten chains in width (five chains on each side of right-of-way) on which the beetle-killed trees were examined, marked, and mapped as they were on sample plots. He also tested out the road strip method on the Black's Mountain Experimental Forest of 10,000 acres which had been previously covered by a 100 percent loss cruise. The results of the sample road strip survey on Black's Mountain gave an estimate of 112 board-feet loss per acre as against an actual loss of 102 board feet per acre obtained by a 100 percent cruise. The time required to make this road strip survey was three man-days as against 75 man-days required to make the 100 percent loss cruise on foot. Conditions for the road strip survey were ideal on the Black's Mountain area because of the availability of a comprehensive network of service roads.

In 1941 Johnson (U119) established road strips to replace the rapidly diminishing number of permanent sample plots in northeastern California. In order that the data from the strips would be comparable in accuracy to that obtained from the sample plots, Johnson outlined the considerations for the selection of strips and standardized the instructions for measuring and recording data. These instructions were designed for the setting up of road strips so that they could be surveyed year after year in the same way as sample plots are used for a continuing loss record.

> "To eliminate non-timbered and overlapping areas along roadside sample strips, 'net length' is defined as 'the timber length of that portion of the strip actually cruised,' while 'gross length' includes net length plus any non-timbered or atypical stand... Each strip should be sub-divided and cruised in units of one mile... If strips are to be permanently marked, one must at least begin the strips at known landmarks or from permanent markers along the road.
>
> "The width of strip is usually governed by the density of the stand and ground cover and by the topography of its cross-section. In the level comparatively light stands of the eastside region, a strip 10 chains wide (5 chains on either side of the road) has been found to be very satisfactory. In the steeper country and denser stands along the westside of the Sierra, it has been found that strips having a total width of more than 5 chains (2½ chains on each side of the road) are not feasible except in a very few cases."

The crew and equipment for roadside strip surveys under these instructions consist of two men with a car (preferably a pickup with open seat in the back for spotter); the duties of one man are to drive and keep the mileage, the other, to spot the trees. Special forms are designed for recording distance, position of infested trees along the strip, and the loss data.

While this method of survey is sound in theory and can be used to advantage by well-trained men, it has a number of practical disadvantages and may be subject to considerable error if not carefully done. Often roads do not traverse a fully representative section of the timbered area. Their usual location along streams or ridges, their use as sheep and cattle driveways, and the frequency of wood cutting or other disturbances along roads often subject such road strips to bias and error on the low side.

A test of the road strip method vs. several other standard methods of estimating bark beetle loss on two large units in eastern Oregon yielded estimates only half as great by the road strip method as by any of the others. In this case, no 100 percent cruise of the area was available for a positive check as to which method was the more nearly correct, but as the other methods had proved reliable in the past, it could be reasonably assumed that the estimates by the road strip method were low.

Aerial Methods in Forest Insect Surveys

With the development of observations and mapping by airplane came the thought that aerial methods might be adapted to bark beetle surveys to speed the coverage of large forested areas and to provide a quick, efficient, and dependable method of estimating current infestations. Two general fields of use were envisioned, (1) general reconnaissance, viewing, and strip counts, and (2) sampling of loss through photogrammetric methods. While the possibilities of aerial methods of bark beetle surveys have been recognized for many years, the actual development of aerial survey techniques for western pine beetle surveys have progressed very slowly.

The earliest attempt to survey western pine beetle damage from the air was made by Miller (U188) in May 1925. A photographic-observation plane was supplied by the 15th Photo Section of the Army Air Service and flights were made over the Sierra National Forest in California. Aerial photographs were taken of the Cascadel and Bass Lake units at an elevation of about 9,000 feet above the ground, using a 12-inch focal length lens, panchromatic film with G filter, and exposures of 1/50 second or less. It was found that individual trees could be distinguished on the photographs, but it was not always possible to differentiate the insect-killed trees, particularly those that had advanced to the dark red color phase. A ground check showed that 90 percent of the insect-killed trees still retaining discolored foliage registered in the photographs. Trees with a heavy cone crop, or with needle cast fungus, often registered as insect-infested "white tops." Recently infested trees could not be differentiated from recently abandoned ones. Actually the scale of these pictures was too small to be satisfactory, and, without a ground check, it would have been impossible to estimate the number of dead trees from the photographs alone.

The following year a test was made of aerial spotting and sample plot photographs under eastside conditions. Through arrangements with the Forest Service, a forest fire patrol contract plane was assigned to the Modoc National Forest for a two-day flight over the Happy Camp-Lava Beds area. A typical 40 acres of infested ponderosa pine forest was marked on the ground by white crosses at the corners. Flights were made on September 26 and 28, 1927 with Capt. Boggs piloting the plane and Keen (U137, U136) making the observations and taking both vertical and oblique photographs with a 4x5 aerial hand camera from over the side of the open cockpit. Two dozen pictures were taken, mostly from an elevation of about 2,000 feet above the forest, using panchromatic film, "G" and "X-2" filters, and exposures of 1/120 to 1/155 of a second. The "G" filter gave the best contrast in the yellow beetle-killed trees.

This test of pine beetle surveying from the air showed that it had definite possibilities and also limitations. It could be of great value for general reconnaissance of unfamiliar areas, but spotting and counts by the eye were impractical in large areas of unbroken forest. Sampling by vertical photographs was shown to be entirely practical for red-top surveys, but additional tests were needed to work out many details as to the most satisfactory flight elevations and map scale, comparison with ground conditions, and relative cost.

Later attempts were made by Miller and Salman in 1931 on the Tahoe National Forest and by Struble and Munhall in 1941 on the Sierra to establish estimates by spotting trees from Forest Service patrol planes. The first of these attempts was unsatisfactory because of unfavorable weather, but the latter attempt was made under ideal air conditions. Eaton states (U54):

> "The flight was made at an elevation of about 2,000 feet above the average ground level. One observer tallied the trees that could be seen and the other spotted the trees on a map. A comparison of the two methods showed that one observer had seen half again as many trees as the other. In spite of good visibility, ability to maintain the desired elevation, and good working conditions, the speed of the plane (80-90 miles per hour) was too great to be satisfactory."

In 1942 Eaton (U54) made a comprehensive review of all the attempts that have been made to apply aerial methods to forest insect surveys. He showed the possibilities and limitations of different methods and proposed research to develop sound survey techniques. He also reviewed the work with autogiros in the East for spotting in gypsy moth and Dutch elm disease control and discussed the recent photographic equipment and processes which may be adapted to forest insect surveys.

In 1947 the Portland Forest Insect Laboratory obtained an airplane and the services of a pilot to develop aerial surveying techniques, and standardize procedures. A study was started along three lines: (1) aerial sketch mapping, (2) aerial strip counts, and (3) aerial photography. (U306). Aerial sketch mapping applies largely to plotting outbreaks of defoliators and those bark beetles that kill timber in mass. It cannot be used satisfactorily for locating scattered western pine beetle infestations.

Aerial strip counts can be used for obtaining quantitative estimates of scattered bark beetle infestations. By this method a "red-top" tree count is made through an opening in the floor of the plane. By adjusting the size of the opening, the eye distance above it, and the height of flight above ground, the width of strip can be predetermined. Distance along the strip is determined by air speed and time. This is adjusted by recording the time of flight between two points of known distance on the ground. In the first trials the hole width was set at 13½ inches, the eye level at 40 inches above it, and the altitude above the ground at 980 feet. These specifications permitted the viewing of a strip 330 feet in width. Difficulties were encountered in flying at this exact altitude above rolling topography, and in keeping the plane flying level. Variations in these flying requirements made for variations in the width of strip viewed. The fact that strip counts are limited to trees which have visibly colored, either sorrel or red, limits aerial strip counts to the making of "red-top" surveys, which are counts of past loss. Such surveys do not indicate how much new infestation may be developing in green, as yet uncolored, trees. Such information can only be obtained through ground checking.

Aerial photography has been explored by use of a K-17 aerial camera, with pictures taken at different altitudes and different film and filter combinations, including color photography. Good weather conditions, with bright sunlight, few clouds, comparative calm, and little or no haze are required for good aerial pictures. Due to length of shadows, photography at the 45th parallel is limited to the period May 15 to September 15 and between the hours of 11 a.m. and 2 p.m. The experimental work on aerial photographic sampling for bark beetle surveys, while showing definite promise, has not as yet developed the final answer to this problem.

Spotting infested ponderosa and sugar pines from a helicopter was first tried in the spring of 1950 on the 11,200-acre Fence Meadow control project on the Sierra National Forest, California, where rugged terrain and deep snows made spotting on the ground a difficult and costly undertaking (U304). A four-inch to the mile detailed map of the area was found essential. On this, infested trees were spotted while flying over the area at a speed between 30 and 35 miles per hour and at a height of 100 to 200 feet above the forest canopy. Familiarity with the area and good visibility were found to be essential. The spotting by helicopter saved a lot of unnecessary ground work but,as Struble pointed out, there were a number of obstacles to be overcome before general use could be made of the helicopter as a spotting tool. One thing that was needed was a more powerful machine that could fly more slowly or hover if need be. It was found, however, that the helicopter had definite possibilities for use in bark beetle surveys and in spotting for control projects.

Obviously, the possibilities for bark beetle surveys by aerial methods have barely been explored. With the development of lighter-than-air equipment such as the blimp,which can maintain relatively slow and stable speeds, the conditions for accurate observations can be greatly improved. With the perfection of color photography, which can detect the color phases of green, infested, and dead trees, sample plot surveys from the air should become entirely feasible. It can be expected that aerial work will be a very useful phase of ~~forest-insect~~ forest-insect surveys in the future.

Factors Affecting Loss Estimates Based on Survey Data

The data obtained from bark beetle surveys require interpretation before they can be translated into loss estimates. The variability of the factors that must be taken into consideration before estimates of any value can be formulated has led to a considerable amount of study designed to improve the reliability and accuracy of area estimates, particularly those based on sample plots.

The Percent of Seasonal Loss Which Can Be Found at Different Times During the Season

One of the usual objectives in a sample-plot survey is to find and measure all of the currently infested trees as a basis for estimating the total loss which will occur that year. A second objective is to record as much of the past loss as is needed for a satisfactory analysis of trends. The first objective is rarely, if ever, accomplished because of the fact that, dependent upon the season and timing of the survey, there is always a certain percentage of the recently attacked trees which show little or no visible evidence of attack. Also, if the survey is made in mid-summer or early fall, many of the trees which will be killed that year have not as yet been attacked. Such trees are therefore missed by the spotters and can only be found on subsequent examinations after all the trees have been attacked and have faded.

In 1931 Keen (U142) summarized the survey records accumulated since 1923 from 106 sample plots in the eastside type of southern Oregon and northern California to see how closely these examinations had come to finding the total seasonal loss. The plots could not all be cruised at the same time so the examinations were spread throughout the season from early summer until late fall. As the same plots were cruised year after year, trees which were missed one season were picked up the following year. From these data, Keen constructed two charts. One showed "Percent of total annual loss spotted on any date" (Figure 51), and the other showed "Percent of total winter loss spotted on any date" (Figure 52).

Figure ~~47~~ 51.— Percent of total annual loss spotted on any date, western pine beetle infestations- ponderosa pine type, Klamath Basin, Oregon, 1923-1929.

Figure ~~48~~ 52.— Percent of total winter loss spotted on any date, western pine beetle infestations, eastside ponderosa pine type, Klamath Basin, Oregon, 1923-1929.

(Pages 527a.527b follow)

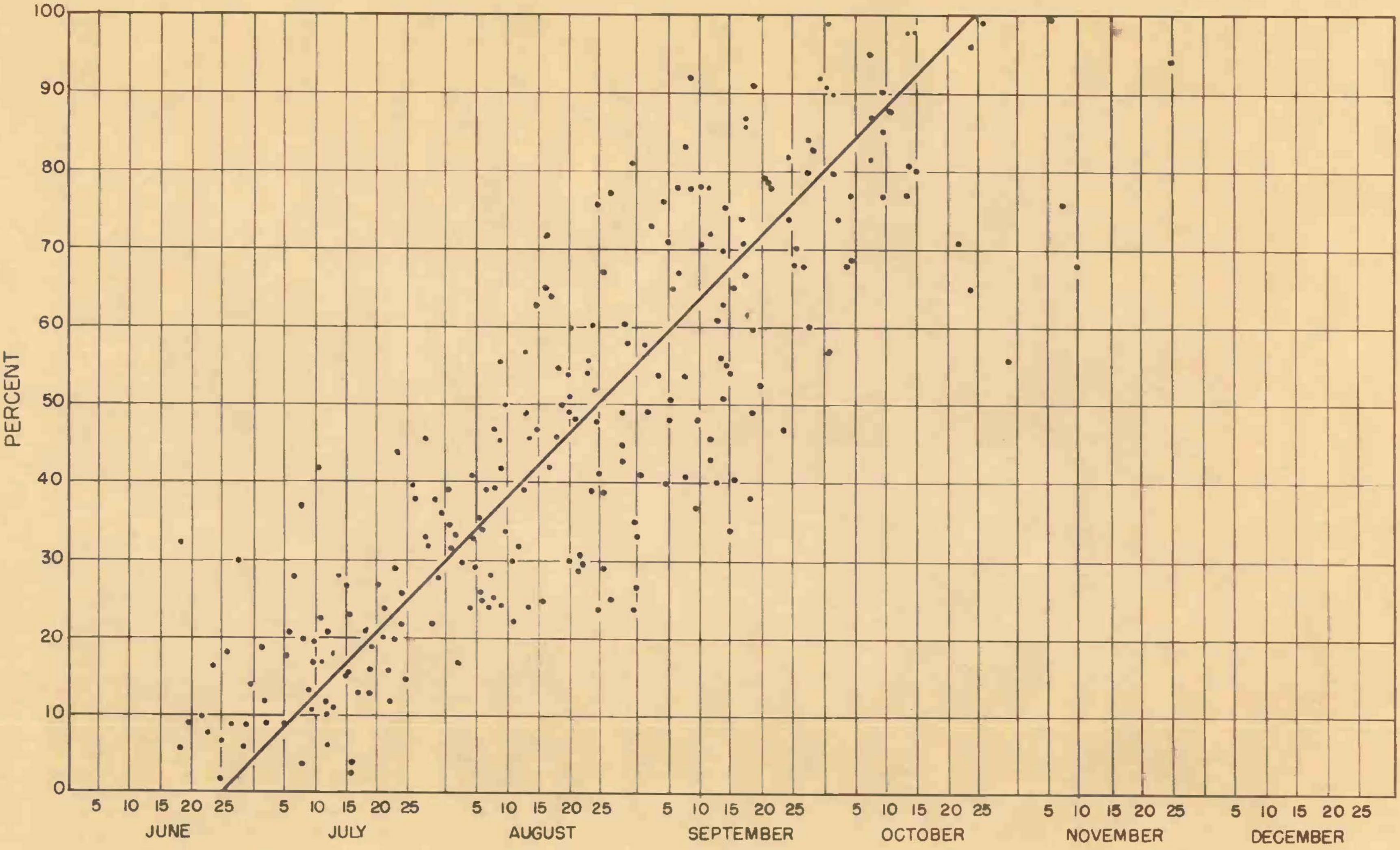


Figure 51.--Percent of total annual loss spotted on any date, western pine beetle infestation-ponderosa pine type, Klamath Basin, Oregon. 1923-1929.

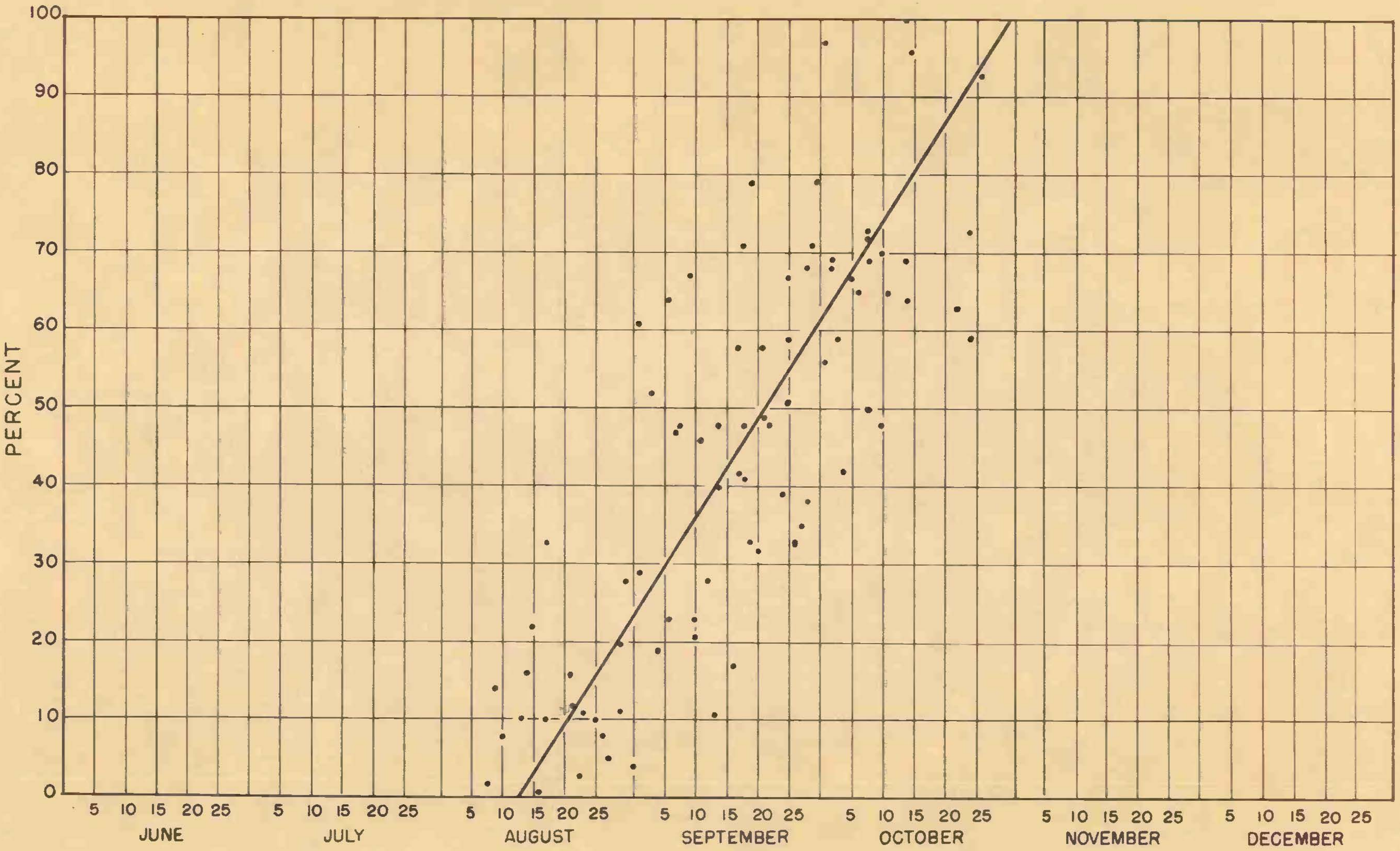


Figure 52.-- Percent of total winter loss spotted on any date, western pine beetle infestations, eastside ponderosa pine type, Klamath Basin, Oregon. 1923-1929

The curves plotted in these charts were shown as straight lines as Keen felt that the variability in loss did not justify a curvilinear relationship. In the instructions for the use of Keen's charts, two methods of estimating the total seasonal loss were offered: (1) add the percentage which was missed as shown by Figure 51 to the visible loss found at the time of the cruise, or (2) if the survey was made after September 1, add to the volume of summer generation already spotted the estimated total volume of winter generation trees as shown by Figure 52. Keen states:

> "In practice the two methods give about equal results. Method 1 tends to overestimate slightly (+ .9 percent) and Method 2 to underestimate (-.3 percent average). Method 1 is somewhat more reliable, having a standard deviation of 16.8 percent, while Method 2 has a standard deviation of 18.0 percent."

In 1935, P. C. Johnson (U118) made a similar study using the sample plot records from the California surveys over the period from 1926-33 as a basis. Johnson prepared separate curves for the Modoc National Forest, the Lassen National Forest, and the westside Sierra subregion; and for different trees, principal insects attacking, and high and low elevations. (Figure 53). Johnson recognized that his curves were supported by limited data, but felt that the flattening of the curves at the beginning and ending of the summer and fall period gave a better estimate than a straight line relation.

Figure 53.— Percent of total seasonal loss cruised on any date: A, Dendroctonus brevicomis Lec. and Melanophila spp. in ponderosa pine, Modoc National Forest, California; B, All primary insects in ponderosa and sugar pine, westside Sierra subregion, California; C, All primary insects in ponderosa and Jeffrey pine, Lassen National Forest, California.

In 1941 Grant (U72) reviewed the work of Keen and Johnson and added to this study the eastside plot records accumulated up to 1940. Grant constructed "a new curve for predicting the annual loss from partial loss data taken during the active period from June 1 to December 20 from a statistical analysis of 1,153 observations on sample plots cruised in the ponderosa pine region of eastern Oregon and Washington during the 17-year period, 1923 to 1939." (Figure 54) The original data all defined curvilinearity and hence straight line regression equations were first computed and then corrected to conform more closely to the data. This procedure was carried out for four subregions, namely Washington, Blue Mountains, Deschutes, and Klamath Basin, and then combined for the eastern Oregon and Washington region as a whole. This new curve[x] is expected to give a better basis for estimating total annual loss than others previously used.

Figure 54 .—Percent of total annual loss spotted on any date. Eastern Oregon and Washington, period 1923-1939. Curve statistically derived from 1153 observations.

(Pages 529a,529b follow)

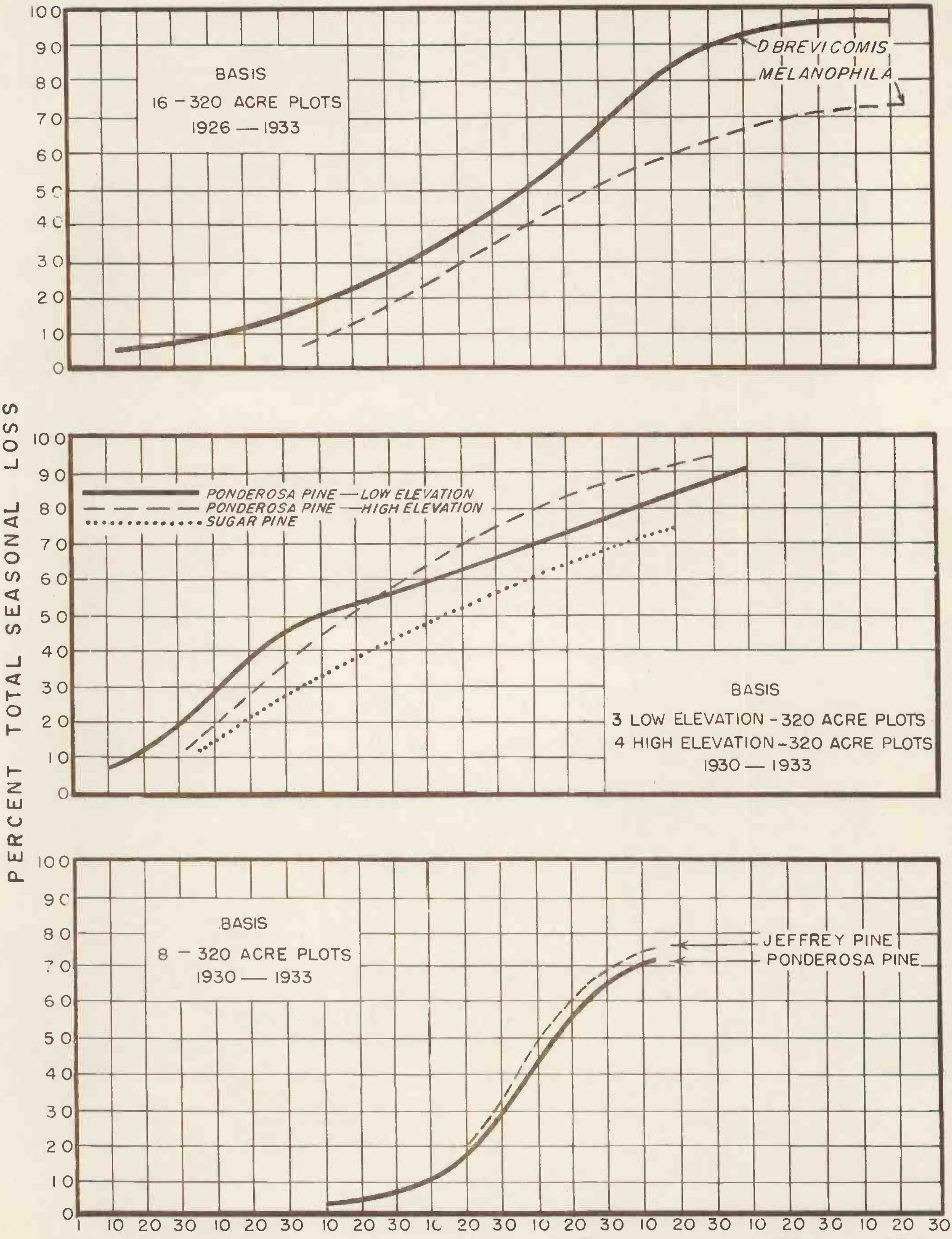

PERCENT TOTAL SEASONAL LOSS
0
10
20
30
40
50
60
70
80
90
100
BASIS
16 — 320 ACRE PLOTS
1926 — 1933
D BREVICOMIS
MELANOPHILA
PONDEROSA PINE — LOW ELEVATION
PONDEROSA PINE — HIGH ELEVATION
SUGAR PINE
BASIS
3 LOW ELEVATION - 320 ACRE PLOTS
4 HIGH ELEVATION - 320 ACRE PLOTS
1930 — 1933
BASIS
8 — 320 ACRE PLOTS
1930 — 1933
JEFFREY PINE
PONDEROSA PINE
1
10 20 30
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

Figure 53

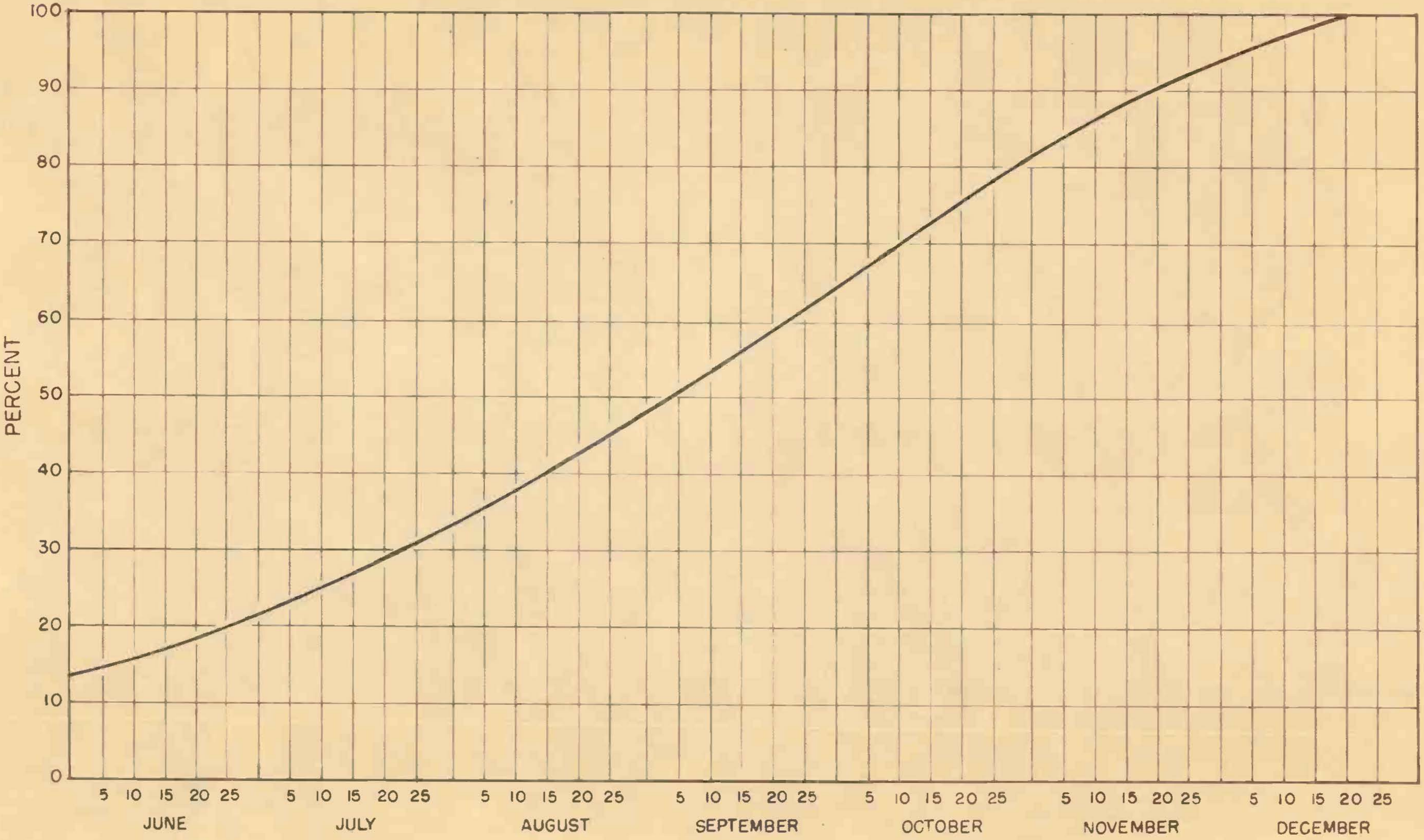


Figure 54.-- Percent of total annual loss spotted on any date. Eastern Oregon and Washington, period 1923-1939. Curve statistically derived from 1,153 observations.

Grant compared his new Region Six estimating curve with the curve derived by Keen for the Klamath Basin (1923-1929), Grant's Klamath Basin curve for the period 1931-1939, and Johnson's curve for the Modoc National Forest of 1926-1933 (Figure 55).

Figure 55.-- Percent of total annual loss spotted on any date. Comparison of studies showing effectiveness of spotting western pine beetle infestations- eastside ponderosa pine type.

(Page 530a follows)

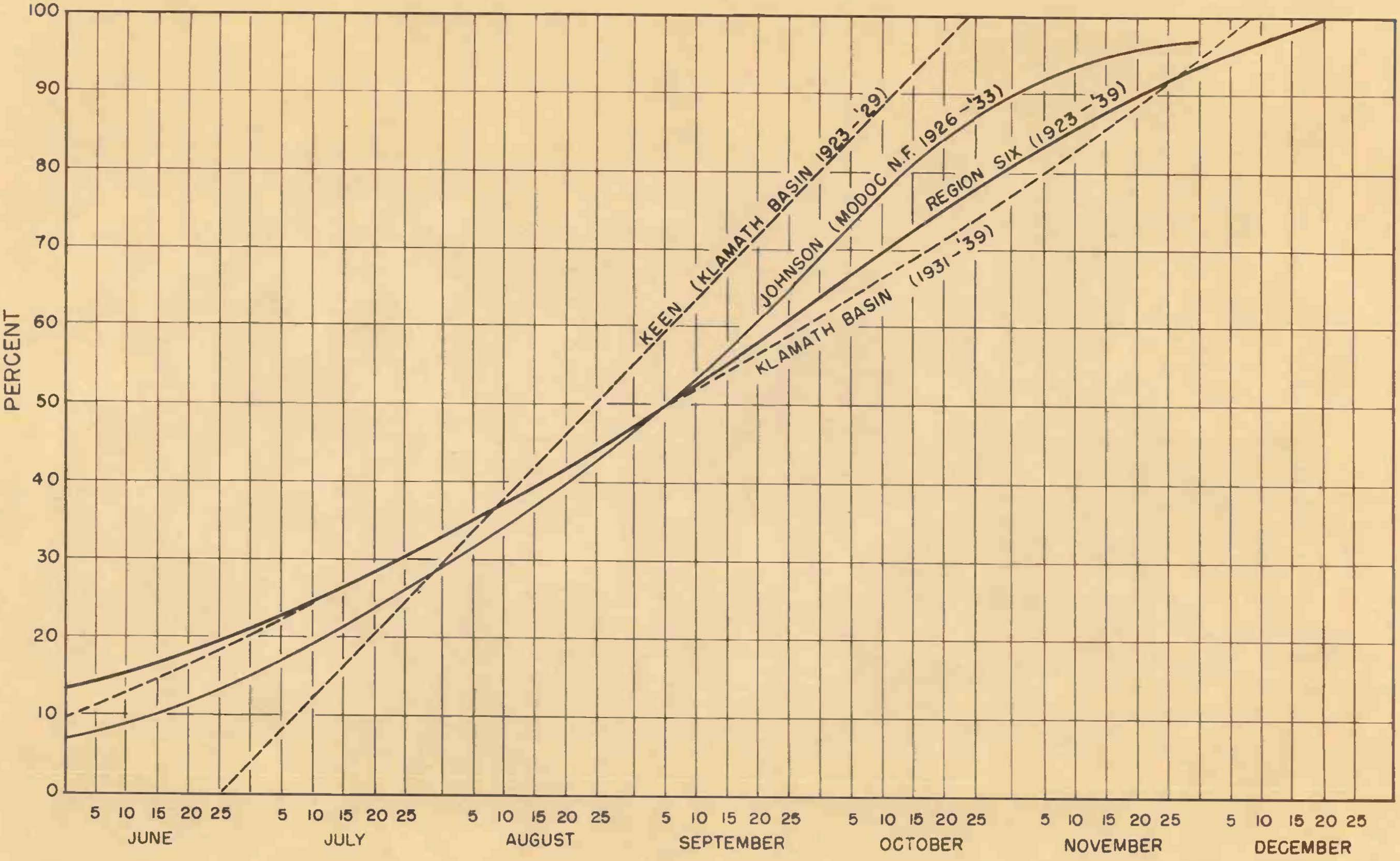


Figure 55.-- Percent of total annual loss spotted on any date. Comparison of studies showing effectiveness of spotting western pine beetle infestations- eastside ponderosa pine type.

Subregional Differences

Grant (U72) found the subregional differences in Oregon and Washington to be of minor significance. "Differences in the four principal subregions were tested and while slight improvement in estimates was indicated, this was not sufficiently great to justify the inconveniences of using four local curves in place of one regional curve."

Elevation

Johnson (U118) compared the curves for ponderosa pine for the higher and lower elevations in the westside Sierra subregions and the different elevations represented by the Modoc and Lassen areas.

> "In general losses occurring at higher elevations appear later in the season and terminate earlier than at lower elevations. The northern forests are fairly uniform in topography and elevation and no correction factor is necessary. It becomes important, however, in the westside region due to ruggedness of the country and rapid changes in elevation."

Composition of Stand

Johnson (U118) considered that mixture of species making up the pine stand may be a factor in modifying loss estimates.

> "The time and rate of development of the losses throughout any one season may vary according to the pine species present, their proportion in the stand, and the primary insect attacking them. Jeffrey pine losses on the Lassen developed throughout the average season at practically the same rate as those in ponderosa pine. On the other hand, sugar pine and ponderosa pine losses on the westside of the Sierra presented different rates of development of seasonal losses. Any estimations made of total seasonal losses would, therefore be the result of two separate estimations; one for sugar pine and one for ponderosa pine."

Trend of Infestation

Keen, Johnson, and Grant all agree that a changing trend in the infestation will cause the actual seasonal losses to be considerably out of line from estimates based on the established curves. According to Keen (U142): "If the infestation trend changes very markedly between summer and winter brood, the total estimated loss on incomplete data may be somewhat in error, especially if the estimate is based on records taken early in the summer." However, this error has not been as large as might be supposed. Johnson states:

> "A sudden increase during or following the survey will normally result in estimating the total seasonal losses too low. To offset this, the percent figure read from the curve for the date of survey must be decreased according to the judgment of the estimator."

Grant discusses this phase more fully:

> "As a general rule total annual loss is apt to be underestimated during periods of increasing beetle activity but this is dependent on the season during which the estimate is made. Epidemics usually progress irregularly and total annual loss is difficult to estimate during early season spotting. It is quite possible that estimates made from a normal curve may be low during the early part of the season and high at the end or vice-versa. In such cases the errors of estimate may be compensated for the year. A knowledge of the effects caused by sudden changes in the infestation and the trend of an epidemic should be more helpful to the estimator during epidemics than estimating coefficients read from a normal curve of total loss spotted on any date."

Seasonal Variations

Keen (U142) states that:

> "In some years when spring comes early and the autumns are late, the period of activity is very long. In other years with late cold spring and a short summer, it has been noticed that attacks are completed much earlier than usual. In such case a much higher percentage of the total loss will be found on any given date than in years when the attack period extends later into the fall. This was particularly noticeable in 1927 when the use of the estimating graph gave an overestimate of approximately 14 percent."

These season variations result in a rather wide spread between years in the date when any certain percent of the infestation can be spotted. This is shown in table form in Keen's report and by comparative curves in the reports by Johnson and Grant.

Author	Region	Period	Spread between dates when 50% of infestation was spotted
Keen	Klamath Basin	1923-29	August 10 to September 9
Grant	Klamath Subregion	1923-29	August 15 to October 15
Johnson	Modoc National Forest	1926-33	August 25 to October 10

Keen found a relationship between the number of clear days and the estimate. A large number of clear days during the year may cause an underestimate of beetle damage. Grant (U72) states:

> "As a general rule it may be stated that any climatic factor which increases the resistance of trees to beetle attack or retards beetle activity will result in an overestimate of total annual loss. Losses are overestimated to some extent when the active season is preceded by very low winter temperatures."

In summing up the effects of seasonal variations, Grant states:

> "Annual variation is largely a function of climatic changes and beetle trends and no correction for these is proposed other than the entomologist's ability to predict the effect of weather and trend of beetle activity from his general observations and past experience."

Errors Due to Time of Year When Cruise Is Made

Keen (U142) analyzed the Klamath Basin data to see when the surveys should be timed to give the most reliable estimates and tabled the results.

Estimates made in	Standard deviation of estimate on any one section	Standard error of estimate for an average of 12 sections
July	81.4% error	23.5% error
August	33.0% error	9.5% error
September	21.4% error	6.2% error
Anytime after Sept. 1	17.5% error	5.0% error
October	13.8% error	4.0% error

Keen's conclusions were that:

> "Estimates made on the basis of early attacks in July will necessarily be very inaccurate. Obviously the accuracy of estimates will improve during the late summer and fall as a higher percentage of total attacks will be evident... It is safe to assume that with a three-man crew after the first of November about 90 percent of the trees will be found if the work is carefully done."

From the Oregon and Washington records, Grant (U72)found that:

> "Spotting has been done generally during August and September on pine beetle surveys and these conditions, as far as estimating total loss is concerned, favor the present practice of making mid-season surveys; namely, the strength of the estimating curve during this period, the small annual variation, and the small subregional variation during midseason."

Errors Due to the Personal Factor

Keen (U142) states that:

> "considerable variation in results will be due to the experience, interest, carefulness, and accuracy of the individual spotters. It has been found that where one man will actually find 99 percent of the infestation evident on an area, another will find only 75 percent."

Keen presents a table comparing the accuracy of the work of five sets of spotters in marking 12,724 trees and concludes that:

> "In the long run, it may be assumed that two spotters of equal ability will mark the same number of trees, or that each spotter will mark half of the total on any section. From the cruises of 106 sections it has been determined that the standard deviation of marking for any one spotter is plus or minus 20 percent."

Johnson (U118) states that:

> "Experience has shown that the efficiency of the average spotter varies with such conditions as (1)training and experience,(2)time of year,(3)speed with which work is pushed, (4)topography and type of infestation,(5)weather conditions, (6)general morale of the men due to living conditions,personality,and willingness to cooperate. Personal errors in spotting will probably always occur,but should be kept to a minimum by the use of experienced men,careful selection and training of new men,and proper supervision of the work."

Errors Due to Methods of Cruising

Keen (U142) states:

> "The intensity of the cruise will make considerable difference. The width of strip, the number of men in a crew, and the rapidity with which the ground is covered are all factors affecting the final result. In one case, a three-man crew using ten-chain strips (five chains per spotter) picked up 50 percent more trees than were found on the same area by a five-man crew taking a twenty-chain strip (five chains per spotter). With the larger crew, the tendency was to bunch around the compassman and leave the outer strip poorly covered. In another case during fall cruising, a five-man crew using a $2\frac{1}{2}$ chain strip each obtained 17.8 percent more trees than would normally have been found by a three-man crew at that time of year."

Methods of Bark Beetle Hazard Surveys

Methods that have been used in bark beetle hazard surveys are at best preliminary and are still on trial. The soundness of any method that is used for this purpose is dependent upon an understanding of the factors that contribute to the hazard of bark beetle attack in pine stands and the ability of the estimator to recognize and appraise these factors. These basic factors have been and still are under investigation and the work that has been done to date on this phase of beetle hazards is reviewed in Section IV . However, such methods as have been used on hazard surveys are reviewed here, although they cannot be considered as final or standardized.

In the northeastern California hazard surveys (93), five ratings of area hazard were established ranging through very low, low, medium, high, and very high. The method by which these ratings were determined have been described in an article published by Johnson (55). The significant factors which were measured in the field were "(1) The percentage of pine volume previously killed by bark beetles; and (2) the percentage of the present pine volume occurring as high risk trees." The data on these two factors were obtained from selectively located strips and the boundaries of each zone of hazard were mapped on the basis of results shown by the sample strips and by visual appraisal through reconnaissance.

In southern Oregon a somewhat different approach was made to hazard ratings by Keen (U151,U159). Using stand, type, and site data made available by the Forest Resources Survey in Region 6, and loss data from a widely distributed series of sample plots and strips, a system of combining these factors through map overlays was devised to arrive at a preliminary appraisal of hazard over rather large areas. Definitions of hazard were on a somewhat different basis from those used in northeastern California.

In hazard surveys conducted in Oregon during 1945-48 (U324,U325,U327), road strips have been used along which counts were made of (1) total stand, (2) number of risk trees, and (3) number of snags. At the same time a visual appraisal of site and stand conditions was made and the area was mapped by five hazard zones in the field.

In 1951, M.M. Furniss (U59) with a field crew carried out a hazard survey of 95,000 acres of old-growth ponderosa pine in the eastern Lassen National Forest of California using the hazard regression formula developed by Keen and Merriam (U164). Cruise lines were located 40 chains apart with one-half acre circular plots established at uniform intervals of 10 chains along a compass line. On each plot data were taken on volume of pine per acre, number of Risk 3 and 4 trees, past loss, and amount of competition from pole stands and brush. Degree of hazard was then computed by formula for each plot and the relative hazards of each unit of the area determined. Due to extensive cutting in the eastside ponderosa pine type, this was one of the few remaining areas of virgin stand in California where hazard surveys would yield information of value in determining order of cutting.

Spotting for Control

"Spotting" is the work of locating, tagging, and mapping the infested trees which are to be cut and treated in control work. The methods used are essentially the same as those used in intensive survey work. The only difference is that all infested trees are visited and marked, the records taken are somewhat different, and all the acreage to be treated has to be covered instead of a sample portion. Two principal methods have been used, (1) the topographic method, and (2) the strip method. Spotting is one of the most important phases of control work, as success depends largely upon finding a high percentage of the infested trees (60).

Topographic Spotting

The topographic method is best adapted to country with steep and well-defined drainages. It is best handled by one spotter working alone. The spotter lays out a definite drainage to be covered each day and by following the ridges or the contours works back and forth along the slopes, marking all the infested trees as they are found and platting them on a map. A good topographic map and a pair of field glasses are aids to this work.

The topographic method has the disadvantage of not covering the area in a uniform manner and some trees are likely to be missed. But it has the advantage of being less expensive than the strip method and is particularly well adapted to rough country where the strip method is impractical.

Strip Spotting

The strip method of spotting is primarily adapted to flat or gently rolling country, or dense forests which cannot be viewed from a distance. Because it is systematic, it is usually more efficient than the topographic method. The advantages are the thorough and uniform spotting of the entire area and the accurate mapping of the infested trees, which in control operations prevents loss of time for the treating crews in relocating the infested trees.

This spotting method is best handled by a three-man crew, consisting of one compassman and two spotters. The compassman carries a line with compass and,pacing back and forth through each section,plots the infested trees as they are called out to him by the spotters, and maps the topographic and cultural features. The spotters work in a strip on either side of the compassman and mark and tally all the infested trees requiring treatment. The width of strip will depend upon the density of the timber stand and the intensity of the infestation. In fairly open stands of ponderosa pine, a five-chain strip can be satisfactorily handled by each spotter. This is the most common width of strip used in western pine beetle spotting. This method of spotting has been done by crews varying in size from one to five men, but the three-man crew is advocated as the best size for spotting in western pine beetle infestations. (Figure 56).

Figure 56 .--A "spotting crew" at work on a western pine beetle control project.

When a spotter finds an infested tree which should be treated, it is conspicuously blazed on at least two sides and a serial number marked on a blaze. Sometimes the tree is tagged with a card or a strip of cloth so it can be easily found by the treating crew. The spotter also records the tree on a "spotting" tally sheet giving its diameter and other information. The tree and serial number is also plotted on the compassman's map in its proper location. Copies of the compassman's map, showing the location of infested trees, are furnished the treating crews, so that the~~y~~ trees can be found and treated.

The amount of country that can be covered by a spotting crew in one day will be governed largely by the number of infested trees which have to be marked on each section, the character of the topography, the amount of detail to be recorded, and the method of marking each tree. In western pine beetle infestations ranging from 50 to 250 trees per section, a three-man crew can cruise on an average 320 acres per day, and spot from 25 to 125 trees. On areas running less than 40 trees per section, and with gently rolling topography and little brush, as much as 480 to 640 acres may be covered in a day. With infestations heavier than 250 trees per section, the acreage that can be covered will be reduced below 320 acres.

(Page 541a follows)

Figure 56.-- A "spotting crew" at work on a western pine beetle control project.

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Spotting is an operational survey which is an essential part of a control job. It is usually handled as a part of the control project and the spotters are under the administrative jurisdiction of the control supervisor. But they are also under the technical direction of the entomologist in charge, who designates the methods to be followed and the types of trees to be marked for treatment.

PLANNING, TERMINOLOGY, AND REPORTING OF BARK BEETLE SURVEYS

Survey Planning

Bark beetle surveys that are comprehensive enough to include large areas usually encounter a wide variation in forest conditions, infestation types, climatic influences, and land ownerships. In order to cover such an area effectively, it is necessary that the estimator first decide how he will go about the job of collecting his data, i.e. what methods of survey he elects to use. Then he will also have to make an organization of the territory, either before or during the progress of the survey, by laying out infestation units which will be of advantage in summarizing survey data and in making control recommendations.

This question of how best to set up the organization of a survey area is one of the first problems in survey planning. It is highly important that this initial planning be carefully and intelligently done, especially for permanent survey programs that are to be continued year after year. Later changes in area organization or methods of coverage, once these have been inaugurated, serve to break up continuity of records and interfere with the interpretation of long-term trends.

Survey manuals now available have focused attention on the techniques of survey work and have largely by-passed discussion of the overall planning of bark beetle surveys. However, underlying much of the work included in the studies of the Lamb's Mine unit (U129), the Rogue River studies (U170, U173, U212), and other earlier surveys, was the attempt to develop the best methods of area coverage and to determine what makes a satisfactory unit for survey and control purposes.

Selection of Survey Methods

The selection of the survey methods that are to be applied to an area is inevitably influenced by (1) the purpose, desired accuracy, and intensity of the data to be collected; and (2) the physical conditions of topography and forest types encountered in the area. In a very generalized way these considerations are outlined by the following table.

Character of data to be collected	Survey methods used
1.Preliminary appraisal of conditions - rough estimates	Topographic method or road strips without measured check plots.
2.Loss estimates of reasonable accuracy for control or management purposes.	
a.In rough country,broken types	Examination and measurement of trees on road strips,supplemented by topographic survey of entire area.
b.Rolling country,continuous type.	Measured check plots,supplemented by road-strip counts or topographic surveys
c.Flat country not easily viewed.	Measured check plots supplemented by reconnaissance and road-strip counts over entire area.
3.Accurate loss data on specific areas for research or control purposes.	Measured check plots,usually of permanent location, often with trees tagged with serial numbers.

Many reporting areas have been found to contain such great variations in conditions that a combination of all methods has been used to arrive at loss estimates. On the whole, no hard and fast rule of thumb has been prescribed for the selection of methods, and the last court of decision always has been the judgment of the estimator as to the method best adapted to the purposes of his survey and to the area he is to cover.

Area Subdivisions and Terminology

It has been common practice to recognize as survey areas land divisions such as national forests, Indian reservations, national parks, timbered areas protected by private owners or under state control in which bark beetle infestations can be treated as a common problem affecting all ownerships in much the same way. For convenience the survey area, which becomes the general area for which the report is prepared, is broken down into smaller units in which infestation conditions can be summarized and analyzed separately.

The indiscriminate use of terms to designate the types of areas used in bark beetle surveys led to a canvass by the Forest Insect Laboratories in March 1944 to see if a uniform set of terms and their definitions could be established. As a result of this the following definitions, which were first proposed by Keen in 1937, were adopted as a guide for the organization of survey areas.

Natural Divisions

Divisions of a forest along geographical, topographical, and ecological lines. Boundaries follow natural divides, such as ridges, rivers, and openings.

Regions.— Major ecological division, such as the ponderosa pine region, the Douglas-fir region, the redwood region, etc.

Subregions.— Major geographical subdivisions of the region, such as west Sierra, northeastern California, Klamath, Deschutes, Blue Mountain, etc.

Divisions.— Major geographical subdivisions of the subregions, such as southern Sierra, upper Deschutes, etc. (This division has only a limited usefulness).

Areas.— Groups of geographically associated units within a division of the subregion; a natural block including several closely related units. (This roughly conforms to a working circle).

Units.— The smallest division of a forested area, based upon entomological considerations; the smallest territory that would have to be considered if control were undertaken. (These considerations will be discussed later).

Administrative Divisions

Divisions of a forest along administrative lines, based upon who manages and protects the area.

Region.— (Forest Service Region 5, Region 6)

Forests.— National forests, Indian reservations, national parks, or large tracts of private land administered by one agency. (These are usually used as reporting areas).

District or "reporting district."— A ranger district or other subdivision of a forest forming an administrative entity, or a block of land which comprises an arbitrary but convenient reporting area (Used mainly in annual reports by forest officers).

Political Divisions

Divisions along well recognized political lines - state, county, township, range, and section. It must be recognized that each of the major divisions is completely independent and only occasionally do the lines of one coincide with the lines of another; for instance, when county or national forest boundaries follow the crest of a mountain range. Therefore, we cannot expect to have natural units and areas conform to administrative or political boundaries.

The Infestation Unit

The first surveys that were made attempted to find an infestation unit which would make an entomologically homogeneous area and which would be independent of adjoining similar units. Miller (U178) defined this conception of the infestation unit at the Third Ashland Conference on forest insect problems.

> "By infestation unit we mean an area in which the amount of infestation will not be materially increased by beetles flying in from outside areas,or decreased by beetles leaving the unit. In other words it is assumed that the factors which influence ,increase, or decrease of beetle populations are operative entirely within the unit itself and are not affected by population changes outside the unit. Two factors then must be taken into account in setting up an infestation unit: (1) effective boundaries, and (2) size of the area. For effective boundaries we are forced to rely upon topographic features, such as high ridges or breaks in type which create barriers that the beetles are not expected to cross in flight. Failing to find effective barriers the infestation unit must consist of an area so large that the amount of infestation which may drift across its borders will not materially increase or decrease the total volume of infestation to an extent that will change trends within the unit."

The ideal infestation unit seems to have been found only in theory. Not enough information on the flight habits of the western pine beetle has yet been uncovered to make certain just what sort of barriers will prevent beetles from leaving or coming into an area. Also we cannot be sure just how far population movements may extend where there are no barriers. Consequently, the selection of infestation units has been based on compromise with a number of factors, some of which are not entomological at all. Factors that have been considered important in the setting up of infestation units are the following:

The Size of the Unit

No standard acreage has ever been advocated for infestation units and as a rule the size of the unit has been determined by the weight of other considerations. This is probably because flight distances have not been established that would warrant setting up any specific acreage as adequate to overcome this factor. The general run of units selected in the commercial pine areas has been 10,000 to 50,000 acres. It seems to have been accepted generally that areas of less than 10,000 acres are too small and that those above 50,000 acres are too large for satisfactory survey and control units. The size of the infestation unit has no doubt been influenced to a very great extent by control considerations, i.e. areas that are adaptable to administration as control units.

Topography

In mountainous country the tendency has been to select tributary drainages of the large rivers as infestation units. Where these tributary drainages are bounded at their sources by high divides with breaks in the pine type and are separated from other tributary basins by secondary or lateral ridges, the boundaries were very easily drawn. Such areas have been considered to be good infestation and control units, especially if they included about 10,000 to 15,000 acres of pine type. Where suitable timber basins have not been available, canyons have been used as the boundaries with the timbered ridges or plateaus between them making up the unit. Units of the topographic type are fairly common in the western slopes of the Sierras and Cascades but are found less frequently in the plateau-like lava formations of the eastside.

Breaks in Type

Breaks in type may consist of open country or changes in the vegetation cover where pine is not an important element in the composition. These type changes are quite often related to elevation, such as rocky, barren ridges on divides, or fir type on higher elevations; and the oak, brush, or desert types at lower elevations. In many areas topography and type changes can both be taken into account in laying out units.

Land Ownership

Ownership has not been given much consideration in laying out infestation units for the reason that this factor has nothing to do with the behavior of the beetles. However, for purposes of control administration, it is at times expedient to consider land ownership in establishing unit boundaries.

Infestation Areas

A natural block of several closely related units has been referred to as an infestation area. Such areas roughly conform to working circles, but in the past have been laid out along natural boundary lines with entomological considerations uppermost and for convenience in connection with control projects.

"Reporting Areas"

This term has also been used more or less synonymously with infestation area, except that the emphasis here is on administrative grouping of units rather than natural ecological groups.

Working Circles

Forest management "working circles" have rarely been used as infestation areas, even though considerable effort has been made to adjust infestation units into the working circle pattern. The trouble is that working circles are usually established entirely on the basis of topography, ownership, and the manner in which the timber will be logged out of an area, and without reference to entomological considerations such as the proximity of related bodies of timber having similar ecological and infestation characteristics.

Even so, the use of working circles for infestation areas can be expected to increase as management plans for the commercial pine stands are perfected and sustained yield units are set up integrating all ownerships under one plan. The advantages of using working circles or "sustained yield units" for infestation areas are:

(1) The boundaries are established for long term use and are recognized by forest officers.

(2) Stand resources have been, or will be, inventoried and growth estimates determined, thus providing a satisfactory basis for determining the rate of depletion caused by insects.

(3) Forest management data on age and composition of the stand provide a clue to the potential bark beetle hazards.

(4) Cutting programs can be modified so as to reduce the bark beetle hazard and thus act as an indirect control against serious losses.

Reporting of Bark Beetle Surveys

The forms that have been used for survey reports have varied from one page questionnaires to long discussions of all the elements involved in an infestation area, depending upon the purposes served by the report and the imagination of the author. Attempts have been made by different forest owning agencies to standardize report forms, and the survey manuals have proposed a number of outlines and forms to be used in survey reporting. Keen (60) gives a complete series of outlines for survey and control reports including:

1. Reports of preliminary reconnaissance of infested areas.

2. Annual forest-insect reports (for use by forest ranger districts).

3. Report on bark beetle estimation surveys of infested areas (separate outlines are given for the first and for subsequent reports).

4. Three outlines are proposed for reports on control projects covering work plans, seasonal work, and the results obtained by control work. The main features of the survey report outline (#3) have been followed in most of the surveys conducted by the Forest Insect Laboratories. The topics covered are:

1. Introduction - history of area, objectives of the survey, and methods used.

2. Survey data - conditions in survey area, insects responsible for the losses, character of the losses, and estimates by units.

3. Conclusions and recommendations.

A perusal of the hundreds of survey reports in the files of the Forest Insect Laboratories and the Forest Service shows that it is very difficult to fit all surveys into a standard or conventionalized form of report due to the great differences in conditions in subregions and areas, and the variation in objectives and perspectives of the surveys. The most informative reports appear to be those in which the author has carefully thought out the points which he thinks are the salient features of the survey, has grouped these points in logical sequence, and has presented them concisely in his own way. Good writing and clear style are as necessary in bark beetle survey reports as they are in any other form of reporting that calls for the orderly grouping of data and their interpretation.

SECTION VI

CONTROL METHODS AND STRATEGY

DEVELOPMENT OF DIRECT CONTROL TECHNIQUES

The first methods proposed for the control of this beetle were direct and involved nothing more than the killing of beetle populations. It was considered necessary (1) to find the trees in which the broods were concentrated, and (2) to cut these down and destroy the infested bark by burning or other measures. The theory behind these methods was that beetles so destroyed could not kill any more trees; and that if the work is done thoroughly over a large enough area, the amount of timber killed subsequently will be reduced to negligible proportions. One condition favoring this strategy was the long overwintering period when the broods are dormant in certain trees; and by finding and treating such trees workers can reach practically all of the beetle population over a fairly large area. The method had its disadvantages in that little, if any, of the infested material could be utilized, since the burning method chars the logs and the rapid development of checking, stains, and rots soon renders most of the treated material unmerchantable. (7).

The idea of using methods to protect the living tree from attack, such as are employed at times for park and shade trees, was dismissed for commercial pine forests because of the practical difficulties encountered in using intensive methods over large forest areas. Even if repellent or toxic sprays could be developed, they would have to be applied on such a scale that costs would be out of line with any possible benefits. Consequently the strategy of destroying the beetles, rather than protecting the trees from attack, is the one that has been followed over the long period of years covered by control operations. It was not until recently that the indirect method of removing the more susceptible trees from the stand by sanitation-salvage logging was evolved.

Under the strategy of control through population reduction, it is obvious that, other considerations being equal, the method which will kill the most beetles at the lowest cost will be the most satisfactory. One of the first requirements is that the equipment used be light enough to be carried around in the woods, and that the techniques employed can be mastered in a short time by the type of labor available in forest and lumbering communities. Quite a variety of methods for killing the beetles have been proposed and developed; and the selection of any particular method is usually governed by the conditions where it is used - the more important factors being costs, ground cover conditions, fire hazard, and effectiveness of the method against the type of infestation encountered.

Of the numerous methods of killing beetles which have been tried, only a few have been found to be practical. The following review takes up all methods that have been tested in order that the record of trial and error may be complete.

The Fell, Peel, Burn Method

This was the first method to be used and has been the one most frequently used on western pine beetle projects. Nothing has yet been found that will kill beetles as effectively and as cheaply as fire. Hopkins (43) gives only a very brief description of this method as applied to D. brevicomis and species of similar habits:

> "Removing the infested bark and burning or otherwise destroying it is necessary to kill the developed broods of larvae, pupae, and new adults which may be located in the outer bark. The time to do the work is from the time activity ceases in the fall until 2 or 3 weeks before the normal time for the winged adults to emerge and fly."

Specific instructions in the details of the fell, peel, burn method are given by Keen (60) in his "Manual of Bark Beetle Control in Western Pine Forests," pages 27-31. Keen states that: "This method is applicable to the treatment of any bark beetle infestation and is the method most widely used on account of its cheapness, its effectiveness in disposing of the beetles, and in cleaning up the slash that results from the operations."

Figure 57 .— Peeling the butt end of an infested ponderosa pine log preparatory to burning the bark.

(Page 555a follows)

Figure 57.-- Peeling the butt end of infested ponderosa pine log preparatory to burning the bark.

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In current practice, the method consists of felling the tree, limbing it, peeling the infested bark from the top half of the down log, and allowing the loosened bark to pile up along the sides of the log. A fire line is then constructed around the entire tree and the pile is fired. By the time the bark is completely burned, the lower half of the log is charred, but the fire usually dies down leaving the heartwood intact.

Figure 58 .--Burning the bark of a ponderosa pine infested with the western pine beetle.

(Page 556a follows)

Figure 58.-- Burning the bark of a ponderosa pine infested with the western pine beetle

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Improvements in the techniques of burning infested bark were developed with experience. One of the first of these applied to modifications of the peeling procedure. At first the entire log was peeled, but it was found that on many trees the infested bark adhered so tightly to the sapwood that the peeling process was tedious and time-consuming. Some attempts were made to treat these tight-barked trees without peeling by piling the limbs and other fuel material over the log and creating a very hot fire. It was soon found, however, that this additional heat had very little effect upon the brood on top of the log where the up-draughts of the fire and the heat-insulating properties of ponderosa pine bark prevented the production of sufficiently high temperatures to kill the broods. Only along the bottom and lower sides of the log where the fire was banked between log and ground was there an effective kill in the unpeeled bark. The peeling practice was finally standardized by peeling the bark only on the upper half of the log, and leaving it intact on the lower half; the peeled bark was then raked in tightly against the sides of the log and set afire. Where the fire hazard was low, the limbs were thrown over the top of the log and burned in the fire; where the fire hazard was high, all excess inflammable material was excluded from the fire lines and only the infested bark burned.

Effectiveness of the cut-peel-burn method depends to a great extent upon finding and treating all of the infested trees in the control area. However, it is hardly ever possible to attain 100 percent spotting efficiency for reasons discussed in Section V ,pages 526-536. Infested trees often are missed on control operations and left untreated, so that from these trees new beetles later emerge to reinfest the area.

A study of the amount of reinfestation developing the first season after control was made by Keen on the southern Oregon-northern California project. On 29 treated sections that were studied a rough correlation was found between the number of trees missed in spotting and the amount of new infestation that developed. The most striking feature of the graph (Figure 59) is the wide variation in the amount of reinfestation where from only 5 to 15 trees were missed per section. However, where more than 20 trees per section were missed, the amount of reinfestation was consistently high. Natural control factors, or the lack of them, undoubtedly account for much of the spread of points shown on this graph.

Figure 59 .--Relation of missed trees to subsequent reinfestation following direct control by the cut-peel-burn method. Southern Oregon-Northern California Pine Beetle Control Project, 1922-23.

(Page 558a follows)

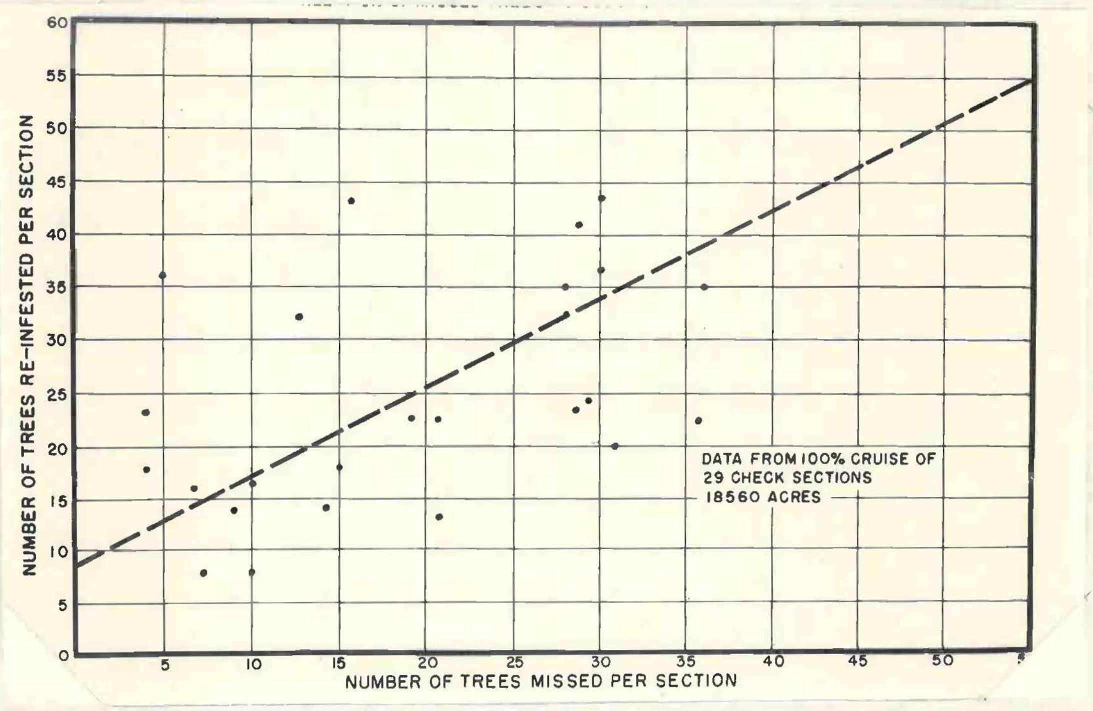

Figure 59.-Relation of missed trees to subsequent reinfestation following direct control by the cut-peel-burn method. Southern Oregon-Northern California Pine Beetle Control Project, 1922-23

The cost of applying the cut-peel-burn method depends largely upon labor efficiency. From a study of the southern Oregon-northern California pine beetle control project, Keen determined the minimum, average, and maximum time required by a three-man crew to cut, peel, and burn a given number of board feet of infested timber. This is shown in Figure 60 .

Figure 60 .—Time required to cut, peel, and burn a given number of board feet of infested timber by a three-man crew.

Minor modifications of this fell-peel-burn technique have been developed to fit special conditions of the infested material and the fire hazard. One common practice is to cut off about 20 feet of the top of the trunk, buck it into log lengths that can be handled, and pile these along the main trunk to help bank the fire.

(Page 559a follows)

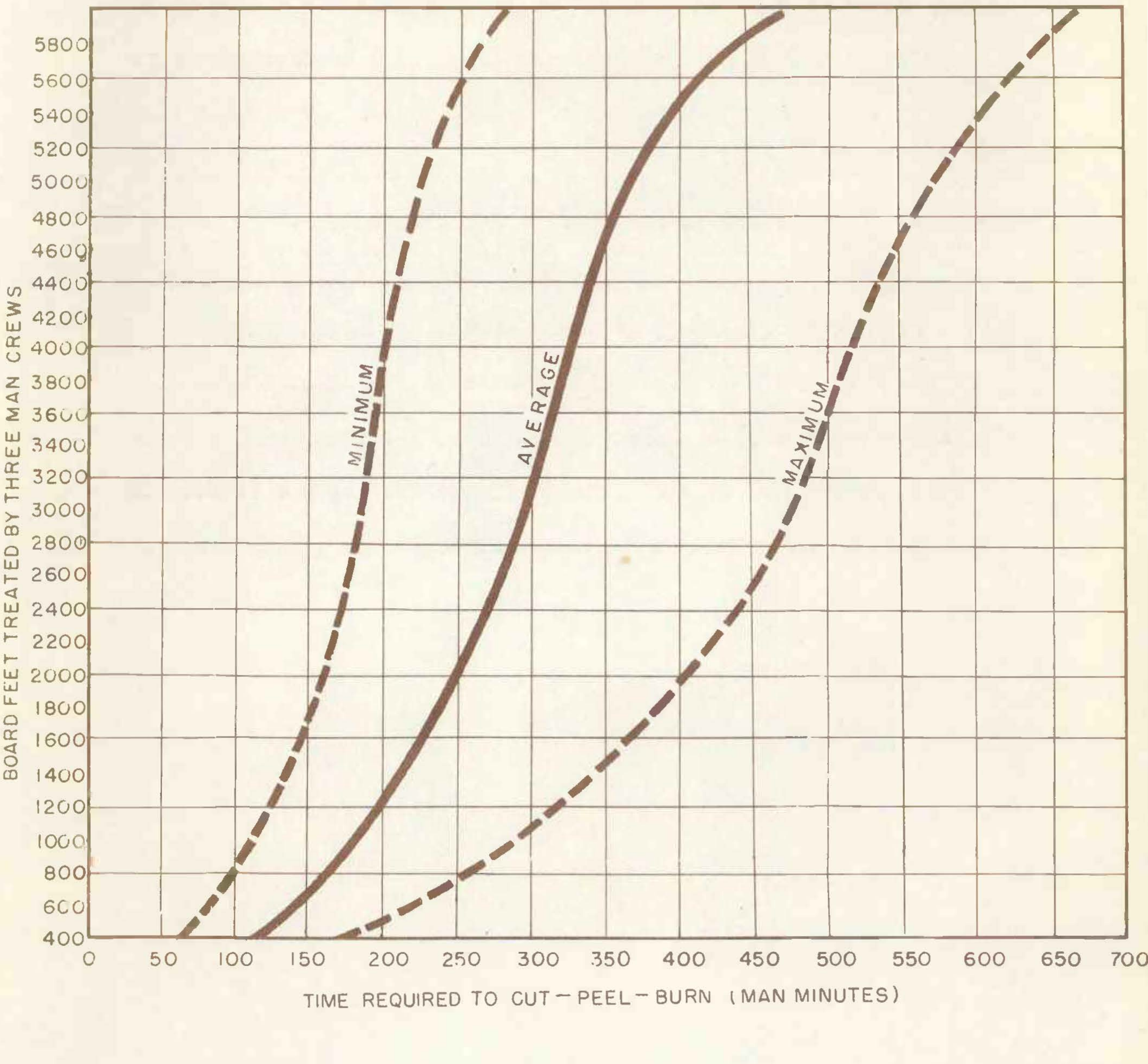

Figure 60.-- Time required to cut, peel, and burn a given number of board feet of infested timber by a three-man crew.

Pit Burning

Control projects using the fell-peel-burn method, which are started in the early fall or extended into the late spring, often encounter dry periods when the bark can be burned only by using extreme care and by taking costly precautions to prevent the spread of control fires. It is also desirable at times to treat summer brood trees in areas such as parks. Under these conditions the practice has occasionally been followed of burning the bark in a pit where the fire can be kept under control. A shallow pit is dug close to the felled tree and, as the bark is peeled, a small quantity at a time is burned in the pit. After the burning is completed, a further safety precaution is taken by covering the pit with soil to prevent live coals from being blown into nearby inflammable material. Pit burning is slow and expensive and is used only when the fire hazard makes its use absolutely necessary.

Decking and Burning

This method was also proposed by Hopkins (43) and has been practiced at times in connection with the fell-peel-burn method. Where the infested trees are grouped and are small enough to be handled readily, it is often more economical to burn the unpeeled logs in piles than to peel and treat each tree separately. The decking method usually requires some additional fuel material to get the fire well started; once underway, however, the heat is banked under and between the logs and the bark is burned entirely. In the larger decks the bottom logs are often entirely consumed, and the top logs settling into a bed of coals are either burned or so thoroughly charred that no beetles escape. Decking and burning is impractical in large timber unless the power equipment is available for hauling and piling the larger logs. In some cases a caterpillar tractor has been used to do the decking (U99). The method necessarily prevents salvage of the treated logs because of the degree to which they are burned.

Use of Fuel Oils to Burn Infested Bark without Peeling

Fuel oils have been tried as an aid to burning the bark on the log, either while the tree was still standing or after it was felled.

The first attempt to use oil was made by the Long-Bell Lumber Company on the Antelope Control Project in northern California in 1921. In this experiment, which was supervised by Charles W. King of the Company and Patterson of the Ashland station, the bark of a standing infested tree was sprayed with kerosene and immediately fired. Although a liberal amount of kerosene was used and the oil burned fiercely on the surface, the heat did not penetrate deeply enough to kill larval broods in the outer bark. The bark itself was charred only where there was an accumulation of resins around an old fire scar. The experiment demonstrated that there was little possibility of effectively heating ponderosa pine bark on a standing tree, since the fire could not be reflected or "banked" against any part of the trunk.

There still remained the possibility that infested bark on felled trees could be burned or heated to lethal temperatures with the aid of a slower burning fuel oil and this was tried in 1932 by Chemist Norman Gay of the Standard Oil Research Laboratory. Gay (35) carried out his experiments in cooperation with the Berkeley laboratory on the sugar pine sale control project on the Sierra National Forest in the spring of 1932. These experiments were well planned; pyrometer readings were kept to determine the degree of heat reached under variable conditions in the bark, such as position on the log and the amount and character of fuel used. Accurate cost records were maintained. As was expected, it was found that bark on top of the log absorbed very little heat, regardless of the amount of oil used; and lethal temperatures were obtained only when enough limbs and solid material were piled over the log to hold the fire for a considerable length of time. The bark on the lower sides was easily burned. Gay's conclusions were:

> "During periods of low fire hazard when all the limbs and other surrounding brush can be utilized to heat the bark and oil used as a supplementary heating medium, we believe that the use of oil will reduce the costs due to the elimination of the peeling operation. During periods of high fire hazard when the size of the fire must be kept to a minimum, we believe that peeling the bark is cheaper due to the fact that all the limbs cannot be utilized to generate heat and an exorbitant amount of oil will be required to effectively burn the bark."

Goop

Another attempt was made in 1946 to improve the oil-burning method by mixing in other materials which would generate a much greater heat than oil alone. This idea was prompted by the success of incendiary materials used in aerial bombing in World War II. One of the most effective of these materials was a mixture known as "goop" which became available in surplus for a few years following the war.

A report by Struble (U297) gives the results of a test made by the Berkeley Laboratory in May 1946, in cooperation with the Army and the Permanente Metals Corporation. The test included large, mature, beetle-infested, sugar pines and ponderosa pines.

Goop is a dark gray, putty-like material composed of finely divided magnesium and magnesium impurities, asphalt, and kerosene. It burns with a very hot flame, which is claimed to produce temperatures between 2000 and 3000 degrees C. In these tests goop was thinned to a desired consistency for spraying or pouring on logs by mixing it with an equal amount of fuel oil. It was found that effective kill of broods under the bark was obtained by the following techniques:

1. Where the bark was less than 3/4 of an inch thick, goop slurry (50 percent diesel oil) alone was applied to the bark surface and burned.

2. Where the bark thickness was greater than 3/4 of an inch, goop slurry was applied as in No. 1, but the top of the log was covered with (a) a layer of pine needles overlaid with 4 inches of moist earth, (b) a 3-inch layer of sawdust, or (c) sheet metal plates. These top-coverings held in the heat while the goop was burning, so that it penetrated through to the brood layer. Of the three types of cover used the pine needle-earth combination was found to be the most practicable.

No further tests with goop have been made, one reason being that the material became unavailable after war surpluses were exhausted. Another important limitation is that its use requires unusual precautions to avoid spontaneous combustion of the goop slurry.

Use of Solar Heat to Kill Broods

Exposure of infested bark to the rays of the sun as a method of killing the beetles developed out of the need of substitutes for burning. The discovery of the effect of solar heat upon the broods and the experimental work that followed have been described in Section II, pages 194-197, under "High Lethal Temperatures." These demonstrations that effective lethal temperatures could be obtained through the use of solar heat opened up possibilities for carrying on control work to advantage during the late spring and summer periods. The method was given a thorough test on the San Joaquin project (83,U180). Practical difficulties were encountered, however, in its application, mainly because of tedious work required to get all the bark spread in locations exposed to full sunlight. The method has since been used only when it was necessary to treat trees during the summer period in parks and areas of intensive use where the expense seemed warranted. The best description and summary of the method has been given by Keen (60).

> "Trees are felled across logs or other objects in order to hold them off the ground. They are then peeled throughout the infested length and the slabs of bark placed in an opening where they will receive the full rays of the sun during the middle of the day. Bark must be carefully spread, and must not be in the shadow of other slabs or trees. On north slopes or in canyons it must be carried out to an opening or propped against rocks or trees in order that the sun's rays may strike it at not less than a 45° angle. To be successful, however, it is necessary to have summer air temperatures of 85°F. in order that fatal temperatures of 115 to 120°F. may be produced in the bark. Such temperatures do not always prevail during the treating season, especially at high altitudes and on northern exposures, and for this reason the results are erratic.
>
> "It can readily be seen that the method is tedious and requires great attention to detail, or it will fail to produce results. In addition this method is more expensive than peeling or burning and is therefore of limited applicability."

Suncuring of the bark without peeling by turning the logs so that all of the infested bark surface finally receives full exposure has been found to be effective with thin-barked trees, such as lodgepole pine infested with the mountain pine beetle. (102). This modification of the solar heat method has been tried with the western pine beetle, but has been found to be impracticable mainly because the thick ponderosa pine bark heats up slowly when attached to the log and because so many of the infested trees are of a size that turning is a difficult and expensive operation.

Use of Toxic Oils to Kill Broods in the Bark without Burning

Although it had long been hoped that a method could be found for killing bark beetle broods that would dispense with both the labor of peeling and hazards of burning, no attempts were made to find an insecticide that would kill the broods in the bark until 1932. In that year, the Standard Oil Research Laboratory at Richmond, California, offered to cooperate with the Forest Insect Laboratory at Berkeley in the development of an insecticide along the lines of an oil spray. The first experiments were started by N. N. Gay (35) who began by testing a wide assortment of materials which were sprayed on infested logs. The main solvents used were mineral oils ranging from heavy viscous grades to the light volatile types. It was found that light distillates caused the highest mortality and that their effect was considerably increased by the addition of soluble insecticides such as naphthalene, creosote, and paradichlorobenzene. An oil-naphthalene mixture, diesel oil of 27 percent API gravity with a saturated solution of crude flake naphthalene, designated as formula number 21046R, gave the best results. This was considered to be the most practical formula because of its general efficiency and low cost.

Gay's preliminary work demonstrated that oil sprays could be used in lieu of peeling and burning and his experiments were followed by a long series of tests conducted by the Forest Insect Laboratory at Berkeley in which the practical limitations and possibilities of the method were thoroughly explored, both in the laboratory and on experimental control projects.

Figure 61 .--Treating a felled ponderosa pine infested with the western pine beetle with a penetrating oil spray.

Salman (U255) tested oil sprays on overwintering western pine beetle broods at the Berkeley Laboratory and obtained mortalities ranging from 22 to 60 percent. Struble (U288) tested the oil naphthalene formula on 39 trees at Bass Lake infested with *D. brevicomis* and *Melanophila gentilis* and obtained mortalities ranging from 13 to 76 percent. This great variation did not correlate with the amount of oil used or bark thickness, [but] bark texture appeared to be the most important limiting factor. (U217).

In 1934, Struble (U289) conducted a series of laboratory tests on bark sections under controlled temperatures and oil dosages. He found no mortality below 50°F., but from 60°F. up to 90°F. mortality increased with temperature and dosage. Also a laboratory experiment by Miller (U195) showed that at a constant temperature of 60°F. mortality increased with time elapsing after treatment and approached 90 percent after 35 days when heavy dosages of oil were used.

(Page 569a follows)

Figure 61 .-Treating a felled ponderosa pine infested with the western pine beetle with a penetrating oil spray.

BEPQ #8602B

When the oil spray treatment technique was transferred to control projects in the field, results were erratic. On the Sierra National Forest in the fall of 1933, (U290) results were so unsatisfactory that the treated trees were burned the following spring. This failure was attributed to low temperatures, thickness, and texture of bark on the large infested trees which predominated on this project.

During 1935, Struble and Hensill (U291) made a thorough investigation of the toxic and physical properties of oils and materials used in different formulae, and brood mortalities were determined for different conditions. Hensill (U90) studied the resistance of D. *brevicomis* larvae to different formulae and the capacity of different oils to penetrate ponderosa pine bark. (Figure 62). The results of the experimental work done was summarized by Hensill (U90), who gave detailed instructions as to methods of application of oil formulae, together with analyses of costs.

Figure 62. Apparatus designed and used by George Hensill in determining rate and depth of penetration of toxic oils in ponderosa pine bark of varying texture.

(Page 570a follows)

Figure 62.- Apparatus designed and used by George [Geo.] Hensill in determining rate and depth of penetration of toxic oils in ponderosa pine bark of varying texture.

BEPQ # 8699A

Two oil formulae were recommended: (1) a creosote-diesel oil-lubricating oil mixture; and (2) the diesel oil-naphthalene mixture (21046R). Larval mortality resulting from the use of the oil-naphthalene formula was found to depend upon the depth and rate of oil penetration into the outer bark. This varied greatly between individual ponderosa pine trees, mainly because of differences in bark texture. Higher brood mortality resulted where brood were in the advanced stages of larvae, pupae, or new adults at time of treatment (U91). The oil apparently did not penetrate directly through the bark, but would creep around bark scales, into ventilating holes, bark crevices, and openings, and reach the larvae through the frass in their larval mines (U92). Results of Hensill's experiments to determine the amount of oil necessary to compensate for differences in bark texture showed that 80 grams per square foot was not adequate, and that extension of time up to 35 days after treatment did not increase mortality of larvae. (Figure 63). A dosage of 120 grams per square foot produced complete mortality within 28 days after treatment. It was shown that the penetrating oil control method could be used to advantage only against broods in thin-barked trees or under special conditions, and that it was impossible to obtain satisfactory control on the bottom of logs unless the logs were rolled and the bottom half given a separate treatment.

Figure 63.—Mortality of western pine beetle larvae in pine bark treated with oil-naphthalene (Formula 21046R) under temperatures ranging from 57° to 61° Fahr. Bark samples of one square foot each.

(Page 571a follows)

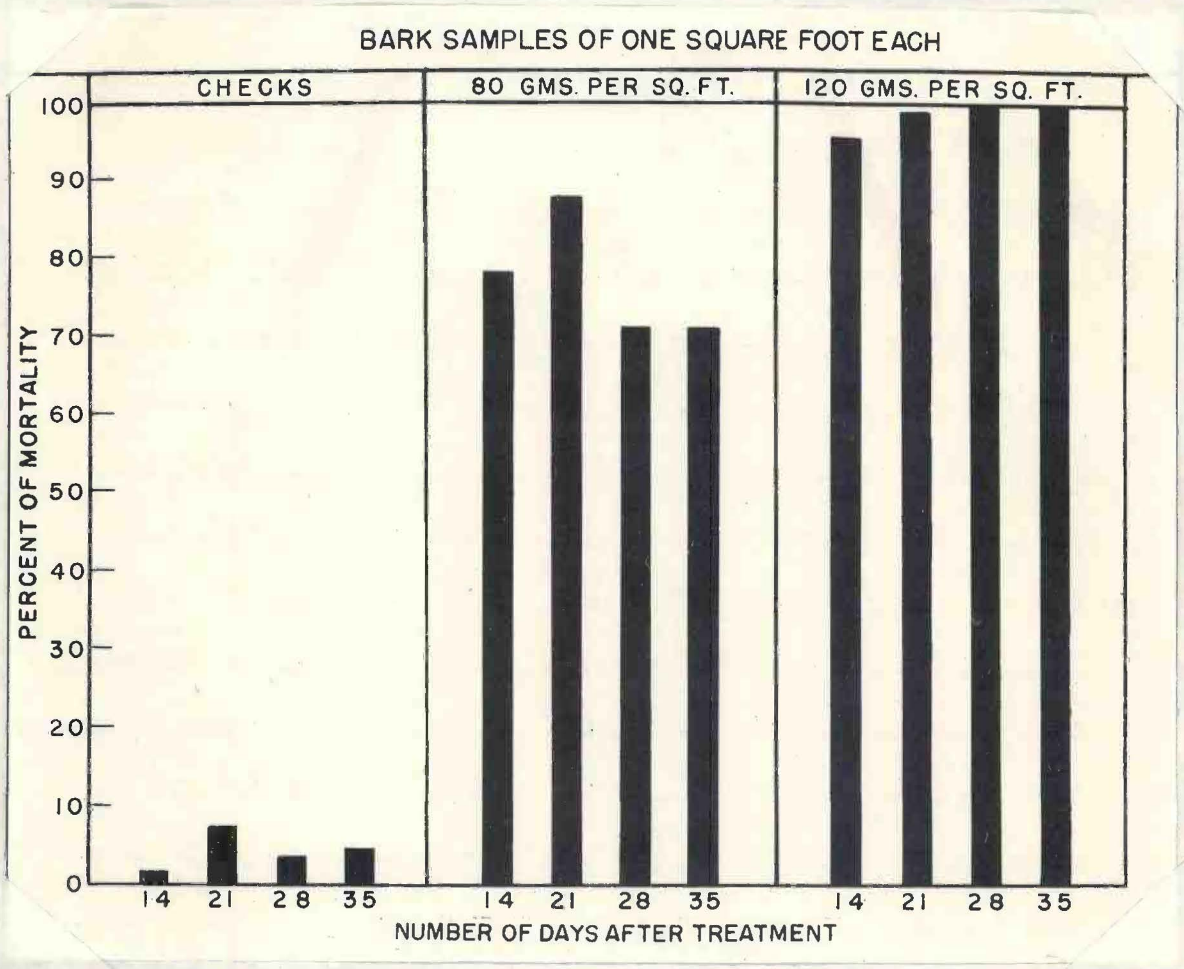

Figure 63.-Mortality of western pine beetle larvae in pine bark treated with oil-naphthalene (Formula 21046R) under temperatures ranging from 57° to 61° Fahr. Bark samples of one square foot each.

In 1938, Salman (112) summarized the conclusions reached in these experiments with penetrating oil sprays. He concluded that:

> "It has been determined that satisfactory mortality of bark beetle broods within or under the bark of infested ponderosa, Jeffrey, sugar, and lodgepole pine trees may result from external applications of penetrating oil sprays. The best control has been obtained with a light distillate type of oil in which crude flake naphthalene has been dissolved at the rate of three-quarters of a pound per gallon of oil. Brood resistance, infestation conditions, temperature, moisture, and thickness of bark cause great variation in the brood mortality resulting from the use of the oil spray. In addition, the difficulties concerned with the transportation of supplies in the forested areas of California and the high cost of the treatment as compared with the peeling-burning treatment limit its use and adaptability.
>
> "Experimental results do not yet justify the general replacement of the peeling-burning method of bark beetle control by the oil-spray method. It may, however, be used to supplement other methods during the season of great fire hazard. The use of oil sprays appears to be of value in recreational areas or in commercial timber when infestation conditions or use requirements make it necessary to control forest insects during the summer.
>
> "The fact that satisfactory results can be obtained by external applications of contact sprays makes further study of the method desirable. Exact studies of the manner in which environmental factors limit the effectiveness of the sprays should be undertaken. Studies of new materials or combinations of materials, and new methods of application should be made in an effort to increase the effectiveness of the sprays and to reduce the costs of application."

The unfavorable factors which limited the use and effectiveness of penetrating oil sprays for control of the western pine beetle were found to be so discouraging that no further attempts were made to apply these sprays against this bark beetle for many years.

Because of the success shown with thin-barked trees, the Coeur d'Alene Forest Insect Laboratory in 1935 took up the investigative work to develop penetrating oil sprays for control of the mountain pine beetle in lodgepole pine and western white pine. This work met with great success and developed the use of orthodichlorobenzene in diesel oil as a most effective spray (U67). A spray consisting of one part of orthodichlorobenzene to six parts of diesel oil became a standard spray for this purpose,and this came into general use for the control of bark beetles in thin-barked trees both in the Rocky Mountain region and the Pacific States.

With the advent of the newer synthetic organic insecticides during World War II, new tests with toxic oil sprays were started in California in 1945 in the hope that some of these very toxic chemicals might prove more effective against bark beetles than those previously tried.

Preliminary tests with DDT in 5% and 10% concentrations in kerosene and stove oil were first made by Hall (2,U82) at the Hat Creek Field Laboratory in 1945 to determine this chemical's effectiveness in killing western pine beetle when used as a penetrating oil spray. Field tests were also run at Harris Springs in cooperation with the McCloud River Lumber Company. The laboratory trials looked promising, but the field tests were not so effective because of thickness of bark and the need to roll the logs to get good penetration on the lower side.

From 1946 through 1949 Patterson continued with a series of tests of these new synthetic insecticides. The experiments included oil treatment of slash to prevent build-up of *Ips* populations, protective sprays applied to living trees to prevent attack, and sprays applied to infested bark surface of logs and standing trees to kill the broods of emerging beetles. The formulae that were tried included DDT, BHC, chlordane, toxaphene, and para- and orthodichlorobenzene in varying concentrations in oil solutions. While the experiments were directed primarily toward the control of *Ips*, *Dendroctonus* beetles were also included in a number of tests in order to broaden the application of results. This work was reviewed by Patterson (U222) in his final report covering the 1949 season. Only slight differences were found in the effectiveness of the different insecticides, but the 5% DDT-diesel oil formula was found to be the most satisfactory. BHC was higher in its initial toxicity;but DDT had greater residual killing power, so the DDT formula was used in most of the control tests. Patterson's conclusions were:

> "Penetrating type sprays were the only kind that gave any promise of success. Results were highly erratic and inconsistent. All the organic insecticides used were highly toxic to bark beetles when in contact with them. Because beetle broods are well protected within and beneath the bark, success in brood destruction is dependent upon the ability of the sprays to penetrate the bark and carry the toxicants to the broods. Penetration of oil diluents is controlled by several conditions, principally by bark texture, density, and amount of surface furrowing. Ponderosa pine offers least resistance to oil penetration, and Jeffrey pine the greatest. There is also wide variation in penetrability of the bark of individual trees of each species, which is not usually obvious from surface examination.

> "Penetrating oil sprays will consistently destroy broods in ponderosa pine bark up to 2 inches in thickness. Control of Dendroctonus beetles was not entirely successful except when the overlaying bark was less than 2 inches in thickness. When thicker bark is encountered, the method is not dependable."

From 1949 to 1952, experimental work on penetrating oil sprays was continued by the Berkeley Forest Insect Laboratory, largely by A.D. Moore, in the forests of southern California, where a method of control which would avoid the use of fire was badly needed. The first tests were run during the summer of 1950, using orthodichlorobenzene in diesel oil (1 to 6 by volume) and DDT in diesel oil (5 percent solution). Tests were made both on felled and standing infested trees. Moore (U203) in summarizing the results of these tests stated: "Good results could be obtained with orthodichlorobenzene and DDT penetrating oil sprays providing trees were felled, bucked into logs, and the logs rolled during treatment so that all of the spray could be applied to the logs from above. Orthodicholorobenzene gave slightly better results than DDT; the penetrating oil spray treatment is not as effective against broods in standing trees as against broods in felled trees." In field tests at Lake Arrowhead during the spring 1951, Moore found that orthodichlorobenzene gave very good results as a penetrating oil spray "where the average size of the infested trees is under 20" in diameter, the bark is thin and dry, and it is not necessary to carry the spray for any great distance."

In the spring of 1951, orthodichlorobenzene in oil (1 to 6) was applied to 50 felled ponderosa pines infested with western pine beetle in the Cedar Grove area of Sequoia-Kings National Park. These trees were too large to be rolled and results were very unsatisfactory.

About 1950, ethylene dibromide was found effective in treating Engelmann spruce beetle in Colorado, and further tests at the Coeur d'Alene Laboratory and in southern Idaho indicated that it had great promise as a toxic spray for control of other bark beetles. L.W. Orr was the first to test ethylene dibromide in fuel oil against the western pine beetle. In preliminary tests undertaken in southern Idaho he obtained very satisfactory control. He stated (1952):[14] "Satisfactory control was obtained when one and one-half pounds of technical grade ethylene dibromide was mixed with five gallons of No.1 fuel oil and applied to the bark of ponderosa pine trees infested with the western pine beetle or mountain pine beetle." These preliminary tests were followed by a large scale application in a control project on the Boise National Forest in 1951. Since 1951 this chemical has been used successfully against western pine beetle on control projects in southern California, and elsewhere.

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[14] In an insert prepared by L.W.Orr for Circular 864 U.S.D.A. (138) at the Forest Insect Laboratory, Ogden, Utah on January 22, 1952.

After twenty years of searching for a satisfactory toxic penetrating oil spray for control of the western pine beetle, it finally appears that an effective insecticide has been found in ethylene dibromide. However, any use of a penetrating oil spray involves careful supervision and attention to details of formulation and application. It is still subject to many of the limitations enumerated by Salman in 1938.

Residual-Type Sprays

With the development during World War II of the newer, synthetic organic insecticides, such as DDT, which kill insects on contact with the crystals, the possibilities arose of applying a thin deposit of one of these chemicals on the bark of pines, to kill beetles on emergence or to protect trees from attack.

Hall (U82) was the first to experiment with residual deposits of DDT as a protective spray on trap trees and logs against attack by the western pine beetle. He found in 1944 that a 2½ percent solution of DDT in kerosene was just as effective as a 5 percent solution in preventing attacks by *D. brevicomis* on green trap trees left in the woods and on logs caged with beetles which were introduced at intervals of two or three days. In addition to *D. brevicomis* the sprayed trap trees killed other insects, such as the common predator *Temnochila virescens* and ants. These tests were continued in 1945 using 5 percent and 10 percent DDT in kerosene and stove oil as penetrating oil sprays applied to infested logs. These tests gave 74 to 98 percent control.

Perry (U223) continued these tests under Hall's direction and obtained favorable results with both DDT and benzene hexachloride in treating *Ips* and *D. brevicomis* in infested tree sections and in protecting trees from attack.

Patterson (U221) carried on a number of field experiments from 1946 through 1949 in which a 5 percent solution of DDT in stove oil and diesel oil was tried as a residual spray against emerging adults of *D. brevicomis*. The spray was applied to standing ponderosa pines as a dense mist in the amount of 4 to 6 gallons of spray per tree to a height of about 40 feet. Patterson found that many of the emerging beetles died in their exit holes on coming in contact with the sprayed surface. Others died from contact with the spray on the bark surface. Patterson concluded that "saturation of the outer bark with DDT will result in death of a high percentage of emerging beetles. Diesel oil with 5% DDT applied to infested stems in form of a mist, or atomized stream, resulted in over 90 percent mortality to emerging beetles."

Residual DDT spray was given a field test on standing trees infested with Ips and D. brevicomis on the Julian-Cuyamaca control project in San Diego County, California in April 1949 by Patterson and Engen (U163). A 3 to 4 percent DDT solution in xylene and diesel oil was applied at the rate of about 3 gallons per tree to a height of 40 feet. While this formulation was applied as a bark penetrating spray to kill broods in place, the residual effect of the DDT deposited on the bark also should be taken into account. The results from caged tests of emergence and attack on green logs were relatively unsatisfactory and erratic.

In 1951, A.D. Moore (U204) carried out further tests with DDT, technical BHC, and lindane, under laboratory conditions and found that all of these materials were lethal to D. brevicomis after short periods of contact (from 5 to 60 seconds). Infested logs treated with a 6% DDT fog showed 96 percent mortality within 48 hours following treatment, while a 0.5% lindane fog only gave a 69 percent mortality in contrast to a 36 percent mortality in checks. Moore concluded that control of D. brevicomis and Ips confusus would be possible through the systematic development of formulations and application techniques of residual type sprays.

Miscellaneous Methods of Destroying Bark Beetles

All of the various ways of killing beetles which have been conceived and tried have not been recorded, as the investigators often dropped the subject when it was found that the results were negative or impractical. Some of these ideas, however, have been reported upon and although they seem to offer nothing in the way of practical possibilities they are listed here in order to complete the record of control experimentation, and for such negative value as they may have.

Scoring the Upper Side of Felled Trunks to Allow Water from Rain or Melting Snow to Penetrate the Inner Bark and Thus Destroy the Broods

This method, which was suggested by Hopkins (43:369),was apparently based on some experiments made by W.F. Fiske with the southern pine beetle. The method was tried without success on the first western pine beetle control project on the Klamath in 1912 (U43). A small series of trees containing overwintering larval broods were felled in the fall and a strip of bark about 4 inches wide was scored for the entire infested length along the top of the trunk. These trees were left over winter and reexamined the following spring. No exceptional mortality was found in the broods; instead, moisture conditions seemed to have been favorable as the larvae had waxed fat during the winter and appeared to be in better condition than broods which had overwintered in standing trees. Other effects noted were that development was considerably retarded over that in standing trees,and the bark,which had been quite tight when the trees were felled,had loosened by spring so that it peeled without effort. However,the results were so unsatisfactory that the method has not been tried since.

Burying Infested Bark in Soil

Covering infested bark with soil was thought of as a method which might suffocate and kill the beetles. In 1923 Miller (U182) ran a test to see if burying infested bark would actually kill the broods:

> "The yellow pine bark sections selected for the test contained about 2 square feet of bark surface. Nine of these sections were collected from the same tree on June 27. The bark at this time contained full grown larvae and first pupae of the western pine beetle. Seven sections were buried in dry soil at depths varying from 2 to 14 inches; as a check, 2 sections were kept under conditions where the brood could develop normally. The new beetles from the check sections had all emerged by August 19.
>
> "The 7 sections that had been buried were uncovered on November 15 and were examined to determine the results. It was found that emergence had occurred in all sections and that the beetles had apparently worked their way out through the covering layer of soil. The bark was then shaved up to see if any percent of the brood had died; the mortality found was but little higher than normal, although the broods had been under ground for 142 days. In the sections buried at a depth of 10, 12, and 14 inches, living larvae were still found indicating that their development had been considerably retarded. No dead pupae were found in any of the sections. Low soil temperatures may account for the retarded development of larvae in the sections buried at 10 inches and below.
>
> "The conclusion is that the method will not work in dry soil. It may be possible to get better results if the bark is planted in moist soil."

The burying method was never given much consideration and has been discarded as a result of this check.

Electrocution

The idea that alternating electrical current could be used to kill bark beetles came to light in the Klamath Basin about 1919. Professor W.J. Chamberlain of Oregon State College made a study of the problem in this area at the request of J.F. Kimball of the Klamath-Lake Counties Fire Association in 1920, and carried out some experiments with high voltage current on infested trees. Chamberlain (18) first found that a current of 110 volts was fatal when passed through the beetles; this was accomplished by placing the beetle on a wet blotter with the two poles of the current very close to the body of the insect. He then located infested trees along the transmission line of the California-Oregon Power Company; these were wired so that the high voltage of the line could be switched into the tree through contacts at the top and near the bottom. Voltages of 6600 and 11,000 were both applied for periods of about 15 minutes. Chamberlain states that "the beetles were killed for some four feet below the upper terminal and some were killed near the lower contact." Apparently the effect of the current upon the broods was quite localized in the bark around the points of contact and was not distributed through the infested bark to a degree that produced any appreciable mortality.

In 1933 the Portland Laboratory cooperated with the Forest Service and the Portland Gas and Electric Company in further tests with alternating current. These experiments, which were suggested by Clay Allen of the Forest Service, were stimulated mainly by the recent development of a light portable generator for the operation of power saws which made it possible to produce high voltage anywhere in the woods. The tests, which were reported by Keen (U145), were made by bringing bark sections infested with D. brevicomis broods into the laboratory where currents of measured voltages and amperes were passed through the sections. Quite a number of tests were run with varying amounts of volts and amperes; but all results obtained were entirely negative. It was found that when voltages were high enough for the current to pass through the bark, it followed the lines of least resistance which were the pitch seams of the bark crevices; as a result, it had no effect in the large bark plates where most of the brood was located. The attempt was also made to kill the beetles in a more conductive medium and wet blotters were used, but it was found that when the current passed through the blotter it did not affect the insects on the surface.

The results of these tests were fairly conclusive that alternating current offers no possibility of bark beetle control, regardless of the amperage and voltages used on infested trees.

Radio Waves

With the development of electronics and the discovery of the lethal effects of high frequency waves upon living organisms, it was inevitable that the idea of trying this on bark beetles should develop. This was tested by Gordon at the University of California in 1934 and reported upon by Hensill (U89). The apparatus was supplied by the University of California. Plates of approximately 12.5 square inches were used and a frequency of 250-300 mils. Infested bark sections were exposed between these plates for periods of 10 to 15 minutes. Some of the results were:

Method of exposure	Mortality
Single bark sections placed flat between plates	100 percent inside plate areas. 0-8.7 percent outside of plate area.
Two bark sections with wood between placed flat between plates	7.1 percent inside plate area. 2.6 percent outside plate area.
Bark section placed end to end (longitudinally between plates)	0. percent inside plate area. 0. percent outside plate area.

The only conclusions warranted from these experiments are that radio waves are effective only within the field of the plates used, that narrow separation between plates is necessary to secure mortality, and that because of these limitations radio waves can be of no practical value in killing the broods in standing infested trees with any of the equipment and frequencies now available.

Fumigation

The use of gas to kill beetles has been considered only in connection with summer control work on the Yosemite National Park. Experiments were carried out to see if an effective fumigant could be enclosed with unpeeled logs by means of a portable fabric cover, the object being to do away with the labor of peeling for solar heat control and the resultant litter of bark spread over the forest floor.

Yuill (U335) tried methyl bromide on bark infested by the western pine beetle in 1938. When infested log sections were enclosed in large plyboard containers, 100 percent mortality was obtained with moderate dosages of the gas; however, when a synthetic rubber fabric blanket was used to cover infested logs on the ground the results were unsatisfactory, mainly because leakage of the gas was so great that mortality was secured only with very heavy dosages. Most of Yuill's experiments were concerned with fumigation of the mountain pine beetle, but the mechanical difficulties which he encountered were equally applicable to the western pine beetle. The difficulties of securing a gas-tight fit of the rubber blanket around an infested trunk on rocky or brushy ground were so formidable that the attempt to adapt this method to the conditions of actual control work were abandoned.

Tree Injection

The introduction of toxic chemicals into the sapstream to kill broods in infested trees has been given a great deal of study in the control of the mountain pine beetle in the northern Rocky Mountain region (4). The use of this method to kill western pine beetle broods has not been attempted seriously, mainly because it was quite evident that the egg galleries of this species cut off circulation in the phloem so quickly after attack that satisfactory distribution of the chemicals seemed hopeless. Gordon (U70) approached the problem by making a laboratory study of the toxicity of certain chemicals which could be used in ponderosa pine to kill broods by means of injection, but did not carry on tests with trees infested by the western pine beetle.

A method for injection of nicotine sulfate into infested trees by a series of bore-holes with inserted pipes was described by Stump (122). It was claimed that when nicotine sulfate was inserted near the base in this manner, the eggs and larvae of the pine beetle were killed and the parent adults that were present left the tree.

The results claimed for this method were so startling that the Forest Insect Laboratory at Berkeley made an investigation of the trees treated by Stump near Mineral, California, and conducted some further tests with nicotine sulfate. This study was reported upon by West (U318). The investigation by Salman and West revealed that the experimental trees described by Stump had been infested by D. valens and not by D. brevicomis; also that several of the trees had died since 1936, apparently as a result of D. valens infestations and chemical injury.

From further tests made by West at Hackamore, California, it was found that:

> "Ten percent nicotine sulfate in sufficient quantities resulted in death of the phloem tissue. Therefore, this compound cannot be recommended for treating living trees. Since there is very little tangential conduction this method (of injection) would not be effective against insects with any compound unless the tree was practically girdled."

The chemicals which have been tried by other than forest entomologists and for which success is claimed would no doubt total up to a formidable list. Dr. A.R. Olson of the University of California Chemistry Department advised the Forest Insect Laboratory at Berkeley (November 10, 1943) that he had successfully controlled western pine beetle infestations in some trees around his summer home at Dutch Flat, California, by injecting 5 to 10 cc. of carbon bisulphide into the cambium layer. This case has not been verified as to species or stage of development of the insect at the time of treatment. Dr. Olson believes that the injection of this chemical would be valuable as a preventive as well as a control treatment. This does not agree with tree injection experiments of the Forest Insect Division which have indicated that non-water soluble compounds such as carbon tetrachloride and carbon bisulphide are not readily taken up in the circulatory system of green trees. (27).

Tree Injection to Preserve High-Risk Trees on the Stump

The theory that injection of toxic chemicals into living susceptible trees would prevent the attack of bark beetles and the introduction of blue-stains and rots has been gone into quite thoroughly for ponderosa pine. This can be considered a method of indirect control in that the idea was to prevent attack on trees that were due to be killed by beetles before they could be reached by logging operations. It was conceded that even if the chemical treatment killed the trees, its use would be warranted if the treatment prevented bluestains and preserved the merchantable quality of the wood until the trees could be converted into lumber.

The method was first tried out on the Modoc National Forest by West (U319) in 1937-38. A series of 50 high-risk merchantable ponderosa pine trees were treated with copper sulphate by the saw-kerf method of injection. During the next two years selected trees were cut and sectioned to see how the chemical had distributed and if the introduction of insects and fungi had been prevented. The results were entirely disappointing. The chemical was found to have distributed very erratically, especially in those trees with decadent crowns. In most of the treated trees a considerable percent of the sapwood was not impregnated. Both insects and fungi attacked the untreated wood. It was also found after the second year that blue-stains had developed even in wood where copper sulfate was present. These conditions, and the fact that checking became prevalent as the trunks began to season, left little merchantable material in the treated trees.

Patterson (U219) continued with this line of experimentation in 1940 in the hope that better chemicals could be found for the purpose and that the erratic distribution could be overcome. Patterson injected some 205 trees using a wide range of chemicals in trees of varying degrees of risk characters. (Figure 64). The plan called for a period of four years on the stump before all of the trees were to be cut and analyzed for the amount of preservation. The final results of these tests were summarized by Patterson (U220) as follows:

"1.*Sapstream conduction of the different chemicals used varied slightly. Sodium arsenite conducted best and copper carbonate least.

"2.Conduction through the sapwood of the stem varied within wide limits between individual trees, regardless of chemical injected or risk characteristics. As a class, low-risk trees conducted slightly better than high-risk trees but the difference was not enough to be significant.

"3. Conduction in trees appeared to be controlled in large part by age of trees and stem length. In general, young trees of small diameter and low to medium height conducted decidedly better than older, larger trees of greater height.

"4. Pitch infiltration in partially transformed sapwood greatly inhibited distribution.

"5. The inorganic chemicals exhibited highly repellent qualities to bark beetles and wood borers; trees treated with the chlorinated phenols were not resistant to attack by these insects. None of the chemicals fully resisted attack by ambrosia beetles.

"6. Blue-stain freely developed in trees treated with all of the chemical compounds used, but it was largely restricted to untreated areas in the sapwood.

"7. Stem checking developed in 30 percent of the experimental trees; checking increased in magnitude and extent with prolonged exposure following treatment.

"8. Stem rot developed in all of the impregnated trees before the end of the final five-year period.

"9. As a result of these tests, the possibility of holding impregnated east-side California pines without deterioration more than three years appears to be remote because of excessive stem checking and rot."

Figure 64 .--Method of injecting wood preservative into high-risk ponderosa pine. Trees with completed rubber girdles filled with preservative in process of absorbing chemicals. ✓

(Page 591a follows)

Figure 64.- Method of injecting wood preservative into high-risk ponderosa pine. Trees with completed rubber girdles ~~and~~ filled with preservative in process of absorbing chemicals.

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Still another application of tree injection to prevent insect attack is the preservation of rustic poles to keep the bark intact on the logs. A series of experiments was carried out by Patterson (U218) to test methods and materials for this purpose. The results with rustic poles were much better than in West's experiments due to the fact that conduction of the chemicals in the younger trees of pole size was much better than in mature high-risk trees.

TRAPPING METHODS OF CONTROL

The idea of trapping beetles by means of light, attractive baits, or trees felled for this purpose has appealed to many workers and some of the earliest investigators carried out trapping experiments.

Light Traps

The fact that bark beetles have not been observed to fly at night did not discourage at least one commercial company from attempting to draw them to light traps. In 1931 Mr. M.F. Postlewaite, agent for a device known as the "Green Cross Trap," installed this apparatus near the California Forest Experiment Station field base at Strawberry, California, in the Stanislaus National Forest. The main attractive element in the trap was the light of either an acetylene or Coleman burner; it also included a water reservoir covered with an oil for which some attractive properties were claimed. The apparatus was constructed so that the insects coming to the light were trapped in the oil and killed. G.R. Struble selected the site for the trap and tended it for six nights during the bark beetle flight period in July. The results of this test were reported in a letter from Struble to Postlewaite which stated that:

> "It looks rather discouraging for the trap so far as bark borers are concerned. The catches to date have been about the same for each night. The insects caught in order of importance are: (1) mosquitoes (males for the most part), (2) other Diptera including gnats, flies, and some crane flies, (3) miscellaneous moths of medium size, none of which are known to be of economic importance, (4) a few aphis and hymenopterous insects, and (5) a few very tiny Coleoptera (flower beetles). None of the bark borers were represented in any of the catches. During the day time, no insects have been noted to be in the traps."

Bait Traps

The idea of using a chemical to attract the western pine beetles to a mechanical trap where they could be destroyed has long appealed to forest entomologists as an easy method of control. The well-known habit of the beetle to concentrate in certain trees and avoid others offered some possibilities for the success of this method, as it indicated that the beetles responded readily to some odors or esters peculiar to slow growing or weakened trees. If this odor could be produced synthetically, it seemed quite feasible to attract the beetles to traps in much the same way that the Japanese beetle is trapped by geranoil. This was one of the motivating ideas behind the long series of studies dealing with attraction of the western pine beetle (see Section II ,pages 102-112). In experiments by Mirov (U202) and Person (U236) mechanical traps were used under insectary control which did succeed in trapping beetles to some extent, particularly when the traps were baited with fermented phloem. However, no chemical substance could be isolated which was as attractive as the natural phloem of slow growing or weakened trees; it was, therefore, considered improbable that a trap baited with fermented phloem could compete with the attraction of high risk trees in the forest. An artificially baited trap might fool a few beetles, but even under insectary conditions it failed to fool all of them.

Trap Tree Control

Trap tree control was first defined by Hopkins (43):

> "The well known attraction of many species of European Bark beetles to weakened, dying, and felled trees suggested to some of the earlier writers on forest insects a method which since that time has been widely recommended and under certain conditions and for certain species of bark beetles has been widely practiced. It is the so-called trap tree method in which living trees are deadened or felled at the proper time or season to attract the insects and induce them to breed in the bark where they can be easily destroyed by removing the latter or burning the entire tree."

However, Hopkins does not give the trap tree method an entirely clean bill of health, since he adds that trap trees may "not attract the beetles to the trap trees, but to nearby healthy trees; thus inducing instead of preventing a destructive outbreak."

Hopkins (43) considered D. brevicomis to be very easily attracted to trap logs and a species that would respond to this method of control. He states that:

> "Under certain conditions, as in the case of logging operations and where only a few scattered trees are infested, it may be desirable as a means of maintaining control, to provide a few trap trees to attract the first generation. This can be done by girdling two or three inferior trees to the heartwood or girdling them in June. Then, if they become infested with this beetle, the bark can be removed from the main trunk and burned by the middle of August. Trap trees to attract the second generation should be prepared in August and September and barked before the first of the following May. Usually an average of one to three trees to the acre should be sufficient for this purpose. However, the number will depend largely upon the prevalence of the insect."

These suggestions by Hopkins led to serious considerations of the use of trap trees during the early development of western pine beetle control. According to Miller (U185), who summarized the attempts at trap tree control:

> "The trap tree differs essentially from the standing infested trees in that when it is attacked the sap flow has been checked and natural resistance in the tree is lowered or entirely lacking. A few beetles can successfully attack and develop broods in a felled tree whereas numbers of beetles must concentrate on a standing green tree with normal resistance in order to overcome the sap flow and make a successful attack. It has been found that the numberof attacks per square foot of infested bark surface in windfalls or felled logs varies greatly and is from 50 to 70 percent less than the average for standing infested trees. It was also found that the emergence of new beetles from trap trees is usually about 50 percent less than that in standing infested trees."

At first glance the trap tree method of control seems to offer definite practical advantages which can be summarized as follows:

(1) By careful selection of trees used for traps, beetle populations can be drawn into inferior or unmerchantable trees and thus prevented from attacking valuable trees in the stand. Trap trees can be used both as a method of bark beetle control and as a means of stand improvement.

(2) Nature at times provides a considerable amount of trap tree material in the form of windfalls and snowbreak. If these are treated at the proper time,they can be used to supplement selected trees and thus add to the volume of treated trap tree material within an area.

(3) Traps can be used to localize the infestation at accessible locations within the area to be protected and thus reduce the cost and difficulties of treatment.

Girdled Trees as Traps

Hopkins suggested girdling trees for traps and at first this was thought to be the best method of attracting the beetles. Chamberlain also strongly recommended it (17). However, the first attempts to use girdled trees were so discouraging that the idea of using this type of trap tree was soon dropped. Miller (U185) summarized experiments with girdled trap trees on the Ashland and Northfork studies.

> "Girdled trees were found to attract beetles only after a considerable interval of time. One tree which was bark girdled in 1916, i.e. the bark peeled to the depth of the sapwood entirely around the base in a band about three feet wide, remained green and up to 1920 had not been attacked. Trees girdled to the heartwood were eventually attacked, but in the case of two trees so girdled at Northfork in April 1920, no attacks occurred until the fall of 1922."

Felled Trees as Traps

Keen (U122) kept records on 17 trees which were felled for traps on the Ashland area in 1916.

> "Although the trees were intended to attract D. brevicomis, they succeeded in attracting for the most part large broods of Ips confusus, Ips oregoni, and Ips emarginatus; leaving comparatively little area for D. brevicomis."

Most of these trees, however, were cut during April and May and were, therefore, exposed to the early emergence of Ips beetles before the western pine beetle was in flight. Keen concluded that:

> "The trap tree experiment was a failure as far as drawing in broods of D. brevicomis from any of the surrounding areas. However, the broods which did attack these trees failed to produce the progeny which is normally produced in standing trees."

Further tests of trap trees were conducted on experimental control work on the San Joaquin project and the Sequoia National Park during the seasons of 1919-21 (U180, U185). Felled trap trees were cut at different periods throughout the season to see if their attractiveness differed with the dates of cutting. It was found that only a small percent failed to attract the western pine beetles within 4 to 25 days if felled between April 15 and September 15. As a rule trees felled after September 15 draw very light attacks or none at all and were not fully infested until the flight period of the following spring.

The Sequoia and San Joaquin projects brought to light the fact that trap logs exposed fully to the sun during the summer months were seldom attacked on tops and sides and were generally unsatisfactory as traps. On the other hand, logs placed in shaded sites were more completely attacked. This condition was reversed during the late fall and early spring periods when trap logs exposed to the sun on warm sites were preferred by the beetles to those in shaded cold sites. This discovery led to the practice of using the branches and limbs to cover traps felled during June, July, and August because shading of the trunks increased their attractiveness to the beetles. The trees were limbed after falling and the branches draped over the down trunks so as to form a screen. If a tree did not have enough top to make a complete cover, then brush, pine needles, or any other available material were used to make a shade for the entire length of the log.

Distance of Attraction to Trap Trees

This question is tied up with the distances that beetles may fly and also with the potency of the trap log to attract them. In a large infested area there is no way of telling just where the beetles come from to attack a trap or how far they may have traveled. Flight distances are discussed in Section II pages 122-140, and records are presented to show that in a few cases beetles have been attracted to trap trees placed outside of the pine type for distances of one to two miles. These records indicate that the attraction to a trap tree is a strong one, but they shed very little light upon flight distances to traps within the pine type where susceptible green trees compete with the traps as centers of attraction. This question can be answered in part only by the results of trap tree studies which will be discussed under "Influence of Trap Trees on Surrounding Infestation, San Joaquin Project."

Use of Trap Trees to Supplement Direct Control Work - The Antelope Project

The first attempt to make use of trap trees on a large scale was made by the Weed Lumber Company in northern California. In 1921 this Company began a control program over 52,000 acres of eastside pine type on what was known as the Antelope Project. The project extended through three consecutive years. Reports by Patterson (U210) show that extensive use was made of trap trees on this project.

Comparative volume of standing trees, trap trees, and windfalls treated on the Antelope control project, 1921-23.

Year	Standing Trees Treated		Trap Trees Treated		Windfalls Treated	
	Trees	Volume	Trees	Volume	Trees	Volume
1921	3,530	2,594,550	660	551,610	163	204,740
1922	1,623	1,444,830	376	359,060	-	-
1923	93	76,760	80	48,190	-	-
Total	5,246	4,116,140	1,116	958,860	163	204,740

The strategy behind the use of trap trees on this project was to follow up the initial clean-up of overwintering infestation by the cut-peel-burn method with maintenance work during the summer seasons to destroy summer broods. It was believed that trap trees could be treated more cheaply and effectively and with less fire hazard than standing infested trees. The traps were felled, covered when necessary, and treated either by burning or sun-curing. As the infestation was greatly reduced by the third year, only a very few traps were prepared and control work discontinued after they were treated. Because of rapid logging of the area, further maintenance work was deemed unnecessary. According to Patterson: "Two series of traps were used in 1921. One series was felled in June and one in September. Only one series was felled in 1922 and this was felled in June."

> "The number of trees felled in each series was based on an estimate of the amount of the first seasonal infestation following the last intensive work. This number was approximately 12 percent of the estimated recurring infestation.
>
> "All trap trees felled were more or less heavily attacked soon after they were placed. In the trees felled in June, the broods developed rapidly and were treated during the latter part of July and August. These trees peeled easily and were treated with a minimum of labor and time. The trees felled in September were not so successful as the broods developed slowly and overwintered in the trees. They were treated with difficulty the next spring.

> "As a successful form of control the method is somewhat doubtful in efficiency. The trees were fairly heavily attacked and no doubt drew and localized a large amount of infestation. However, there was a tendency to create group infestations in standing trees adjacent to traps. This was the noticeable effect of the method on this project; a number of instances were noted where these groups amounted to 4 or 5 standing trees per group."

Records tabled in the first annual report show that *D. brevicomis* attacked 100 percent of the prepared trap trees. However, *Ips* (two species) were also present in 63 percent of the traps, *D. monticolae* in 12.5 percent, and *Melanophila gentilis* in 11 percent.

Influence of Trap Trees on Surrounding Infestation - San Joaquin Project

Trap trees were used on the San Joaquin project to supplement the cut-peel-burn method for two successive seasons (1920 and 1921). During the summer period widely scattered trap trees were placed at selected accessible points where it was thought they would do the most good. Enough trap tree material was created each season to absorb the estimated amount of untreated infestation that was missed in spring control work on the overwintering infestation. During the second season that this method was in use (1921) the volume of infestation in standing trees increased regardless of the available trap material. An attempt was then made to determine how much of the seasonal infestation could be drawn into traps. The experiments that were designed consisted of two phases: (1) after it had been thoroughly cleaned of infested trees, an area was surrounded with a ring of trap trees to see if the beetle would cross over the trap ring in order to attack standing trees within the cleaned area; and (2) a line of trap trees was extended across an infested area to see if their effect in absorbing beetles could be detected within a mile zone on either side of the trap line. Both of these experimental phases were carried out during the season of 1922.

For phase (1) a circular area one-half mile in diameter was selected in the pine type of the Chiquito basin. During the spring control period this circular area was cruised several times and all infested trees that could be located were treated by the cut-peel-burn method. On June 7 a ring of trap trees spaced four chains apart was placed around the perimeter of the circle to absorb the attack of the first seasonal generation. A second ring of trap trees was placed August 7 for the second seasonal generation, and still a third series was placed October 7 for the partial third generation. All trap trees were treated by burning as soon as they became fully infested.

Throughout the season the area within the circle was kept under frequent surveys, and infested trees were treated as soon as they were detected. Under these conditions it was assumed that any trees attacked within the circular area during the course of the season would be attacked by beetles that came in from outside of the circle, and that in order to reach these trees the beetles would have to cross the line of trap trees. Such behavior could then only be explained by the assumption that certain standing green trees within the circle were more attractive to the beetles than the trap tree material. Results at the end of the season indicated that seven large ponderosa pines were attacked within the circle, some of which were located very close to its center.

The second phase of this study was also located in the pine type of the Chiquito basin. The traps were laid out in a nearly straight line about six miles in length. The type was composed mainly of ponderosa pine for several miles on either side of this trap line. The traps were placed eight to the mile (10 chains apart). The first series of traps was felled June 14, the second series August 18, and the third series October 10. The traps were treated as soon as they became fully infested so that no new broods of beetles would escape from them. The mile zone areas on either side of the trap line were cruised at intervals during the season and the locations of newly attacked trees were plotted so as to determine their distance from the nearest trap tree. At the end of the 1922 season the infestation records were summarized for the year that the traps were in effect and also for the year preceding.

Infestation within one mile of trap line before and after the traps were placed.

Year	Volume of trap trees		Standing trees attacked within one mile on both sides of trap line.			
	Trees	Volume	0-½ mile zone		½-1 mile zone	
			Trees	Volume	Trees	Volume
1921	0	0	69	96,870	96	48,200
1922	91	16,000	101	132,750	33	60,080
Percent of increase, 1922 over 1921				+ 37%		+ 25%

These results appear to show only that the traps did not draw beetles away from standing trees to any greater extent in the vicinity of the trap line than from a distance of one-half to one mile. If we can accept the experiment at its face value, the increase of infestation in standing trees was greatest in the zone nearest to the trap line. This trend is further emphasized by the fact that records show that several groups of from 4 to 14 trees were attacked in the vicinity of the trap line; thus indicating that beetles were drawn to the general locality of the trap line where they attacked both standing trees and traps.

Composition of Infestation Drawn to Trap Trees

Both the western pine beetle and associated insects are drawn to traps. As shown by Keen's first studies (U122), the volume of *Ips* infestation attracted to traps early in the season may be large enough to occupy most of the bark surface and thus exclude effective attacks by *D. brevicomis.* The extensive use of traps on the Antelope and San Joaquin projects has yielded much additional data on the composition of trap-tree attack. On the whole, records from hundreds of trap trees have shown that over the entire season *D. brevicomis* makes up the bulk of the infestation, while the attack of associated insects is highly variable both in incidence and intensity. The following table summarizes the percent of trap trees attacked by different insect species on the Antelope and San Joaquin projects.

Percent of total trap trees attacked by *D. brevicomis* and associated insects.

	Antelope project	San Joaquin project
D. brevicomis	100.0	88.8
Ips spp. (*oregoni* and *confusus*)	63.0	32.0
D. monticolae	12.5	1.1
Melanophila (*gentilis*)	11.0	5.9
Not attacked by insects		8.3

The above averages apply to both mixed and pure infestations and do not attempt to make a quantitative comparison of the volume of infestation represented by each species and the mixtures. On the San Joaquin project, records were kept of the various combinations of species found in the traps which give the following comparison of percent of trees involved in each infestation type.

Percent of trap trees attacked by different types of infestation, San Joaquin project

Type of infestation	Percent of total trap trees
Attacked only by D. brevicomis	51.0
Attacked only by Ips spp.	1.1
Attacked by D. brevicomis and Ips spp.	30.6
Attacked by other mixtures	8.6
Not attacked by bark beetles	8.7
Total	100.0

The records also show that types of infestation varied greatly according to the time of the season when traps were felled. Ips attacks were more abundant in the spring and early summer periods, but some Ips attacks occurred sporadically for the most part throughout the season.

The traps which were not attacked by bark beetles were found in all series whether the trees were cut in June, August, or September. The number of trees not attacked was higher in the October series, which may have been due to the fact that most of these late traps were not exposed to attack until the flight period of the following spring; and the changes which took place in the green phloem of down trees during the winter may have made them unattractive to beetles by that time. However, it would seem that there are certain trees which do not attract beetles regardless of when they are cut for traps - just why has not been determined.

Summary of Trap Tree Control

Out of the various trap tree studies and the attempts to use traps as a control method, the following points have been established (MU185)

1. *D. brevicomis* is attracted to nearly all ponderosa pines soon after they have been felled. Certain trees, however, will not attract this beetle even though they have been carefully prepared as traps.

2. Girdled trees do not make satisfactory traps.

3. The attractiveness of trap trees depends upon fairly exact moisture and temperature conditions in the phloem. During the months of June, July, and August it is necessary to shade the upper side of fallen logs in order to induce attacks. In the spring and late fall beetles are not attracted to traps in cold shaded sites.

4. D. brevicomis broods in trap logs produce less progeny than in standing trees. (U122)

5. Associated insects, such as several species of Ips, D. monticolae, and flatheads, are attracted to traps and enter into various combinations of infestation types with D. brevicomis. On general averages throughout the season, however, D.b. constitutes 75 percent or more of the volume of infestation drawn to trap trees.

6. Experiments have shown that trap material even if readily available to the beetles in flight will not keep them from attacking standing green trees that are especially attractive. Beetles will pass over traps to attack standing trees (trap tree circle experiment). Groups of standing trees will sometimes be attacked in the vicinity of trap trees (trap line experiment).

7. Increasing the volume of trap trees will not prevent an increase of infestation when conditions favor this trend, either in the immediate vicinity of the traps or in zones one mile distant (trap line experiment).

8. The cutting of green trees for traps when a sacrifice of timber value is involved is of doubtful value because the control effects are too slight to warrant the waste of timber resulting from this method.

9. Where creation of traps is unavoidable, as in the case of windfalls, right-of-way clearings, etc., the preparation and treatment of this material for traps may be warranted as a control measure. No sacrifice of material is involved and the practice can be used to destroy some of the beetle population in the area.

CONTROL EFFECTS OF LOGGING OPERATIONS

In the earlier phases of bark beetle control studies, entomologists suspected that the trapping effect of green logs on large scale logging operations had considerable effect upon surrounding beetle populations. One operation in Idaho has been reported (page 618) where the logs were intentionally left in the woods long enough to serve as traps. Beal (U4) attributes to Keen the report that "On the southern Oregon-northern California project two of the cleanest areas were adjacent to regions where continuous logging had been in progress for several years; and that, in one unit, a reduction of 60 percent in infestation - equal to the best results obtained by artificial control work - followed the beginning of logging operations on adjacent ground." These and other observations in the pine lumbering areas indicated that regular logging operations do have some effect in reducing beetle populations, but it was not until detailed studies were undertaken that some appraisal could be made of the extent to which green logs may absorb attacks and carry beetle populations out of the woods.

The Studies in Southern Oregon, 1930-32

Beal (U4) started a comprehensive study on lands of the Weyerhaeuser Timber Company near Klamath Falls to determine the effect of logging operations on beetle population in 1930. This was a large logging operation which had started cutting in a unit where the western pine beetle infestation was increasing; the daily output of logs was around 300,000 board feet or 40 carloads, so that green trap material was available to absorb very large beetle populations. Beal's method of attack upon the study consisted of a standard method of log examinations and records designed to show the amount of bark area that had been attacked by the time the logs were leaving the woods. These examinations included 696 trees which were selected as samples of the total amount of green trap material.

In addition, periodic strip cruises were made to determine the trend of the infestation in standing trees on the operation and adjacent territory. Results within the log material were summed up by Beal (U9) in his final report:

> "Attacks on felled trees vary throughout the season and appear to be influenced chiefly by the number of beetles in flight and the quantity of material available. In an operation removing daily 300,000 board feet of lumber, 51 percent of the logs contained beetle attacks after an average exposure of about two weeks.
>
> "The frequency of the attack varied with the exposure from 4.4 percent of total bark examined on the top side of logs to 20 or 30 percent on the sides and 36 percent on the bottoms. The attack varied with the season from 0 in April and October to nearly 50 percent in August, the peak of the flight period."

> "Beetles concentrate chiefly upon the middle and basal portions of felled trees, but in practically all cases keep out of the top sides of the logs. Beetles are sometimes attracted to logs less than 4 days old, but most rapid absorption of beetles occurred on logs from 4 to 10 days old.
>
> "The beetles appeared to concentrate their attacks on definite log groups rather than spread out evenly over all logs on the ground. These favored logs continued to absorb beetles until they were removed from the woods.
>
> "The attractive influence of felled logs is relatively local. Beetles do not appear to be attracted to this material over distances greater than about one-half to three-fourths of a mile.
>
> "It does not appear necessary or especially advantageous to leave logs in the woods longer than about 2 or 3 weeks for the purpose of absorbing beetle attacks. During heavy flight periods and in the middle of summer when danger from bluestain is greatest, they may be removed from 10 days to 2 weeks after felling with considerable assurance of removing a great many beetles with them."

In measuring the effect of the operation upon the trend of infestation within the general unit, the study failed to give conclusive results. The volume of standing infested trees within the unit was relatively high, averaging 177 board feet per acre and continued to increase during the progress of the logging operation. Beal stated:

> "Logging had no apparent effect upon the Clover Station unit as a whole, because on it during 1929 and 1930 the infestation increased irrespective of logging or the trend of infestation throughout the region. This has been increasing at a uniform rate since 1926, three years before the beginning of logging operations. It is self evident that the logging of one-fifth of the entire unit, since it was in a heavily infested portion, materially reduced the total volume lost. However, the losses outside the logged area increased. It will be necessary to continue the surveys over a period of years before the influence of logging can be more accurately determined."

Beal also gave some attention to logs on right-of-way clearings which as a rule were in better shaded positions than those on the main logging area. He found that "right-of-way logs appear to be very attractive to the western pine beetle and to *Ips*, especially *Ips confusus*."

Studies at Black's Mountain Experimental Forest, 1941

In 1941 examinations were made and records kept by J.W. Johnson (U111) on the sanitation-salvage logging operation at Black's Mountain Experimental Forest. In his report, Johnson reviewed the preceding work of Beal, and other studies pertaining to trapping of the western pine beetle. The study was undertaken because it was believed that the light sanitation-salvage cut at Black's Mountain set up conditions that differed as to the amount and nature of trap material from heavy cuttings like those on the Weyerhaeuser operation studied by Beal. Instead of a concentration of logs representing practically all of the commercial stand, sanitation-salvage logs were from selected risk trees considered to be susceptible and composing less than 25 percent of the stand. For the most part these risk trees were widely spaced throughout the green stand. As some low-risk trees were cut for silvicultural reasons, the Black's Mountain operation afforded a favorable opportunity to determine whether logs from high-risk trees were more attractive to beetles than logs from low-risk trees.

Johnson's methods of sampling and recording were similar to those used by Beal, although the volume of material studied was considerably less. A total of 128 ponderosa pines and 3 Jeffrey pines, amounting to a 9 percent sample of all logs removed on the operation, was analyzed. The 1941 infestation on the Black's Mountain area was very light, averaging under 50 board feet per acre; also, the seasonal period of attack and flight was relatively short for that season. These conditions may have had much to do with the lack of pertinent results obtained from this study. Johnson found that:

> "Sixty-six percent of the ponderosa pine logs sampled gave no evidence of attack. Infestations were uneven and one-sided in the logs. The trapping of considerable numbers of beetles in logs seems to depend upon the fortunate coincidence of a number of distinct factors. It could not be shown that sufficient trapping actually occurred in 1941 on most areas treated by sanitation-salvage to markedly affect the beetle population in these areas. The risk ratings given to trees previous to cutting had no apparent relation to their attractiveness to beetles. In a sample limited to 55 trees, the percentage of attack in each risk class was: Risk 1, 23.5%; Risk 2, 25.0%; Risk 3, 33.3%; Risk 4, 12.5%."

(Johnson considered the sample too small for reliable conclusions.)

CONTROL THROUGH LOGGING INFESTED TREES

Removal of infested trees from the woods and their utilization can be considered as a method of reducing beetle populations, providing the logging operation is managed so that the broods are either destroyed or transported to some distant point where the emerging beetles cannot find living trees to attack. Hopkins (43) suggested three optional methods for disposal of the infested bark: (1) transporting the infested trunks a sufficient distance (20 to 50 miles away) from any living spruce or pine, (2) by placing the logs in water, and (3) by converting the logs into lumber and burning the slabs. A number of logging control operations in the western pine region which will be described in the following paragraphs have employed these proposed methods.

Transporting the Infested Logs

Probably the first project to control a western pine beetle infestation by this method was described by Evenden (33). This operation was located on a tract of about 3000 acres in southern Idaho belonging to the Boise-Payette Lumber Company. On finding that from 15 to 17 percent of their ponderosa pine timber had been killed in recent years by the western pine beetle, they moved their working plans ahead about ten years and started cutting the timber in August 1922. Both green and recently-killed trees were felled and removed to the mill some 30 miles distant. The green logs were left in the woods long enough to absorb emerging beetle broods, but not over four weeks, and in this way the bulk of the infestation was removed from the woods. The project closed in the fall of 1923 and in August 1924 an examination of the timber surrounding the cutting failed to show any infested trees within a half mile radius.

Since the advent of truck logging during the 1920's, many projects for the control of western pine beetle infestations have been carried out in which the infested logs have been transported many miles to mills. Usually these projects have included the salvage of recent snags as well as the removal of currently infested trees. From an insect control standpoint they have not been too successful due to failure to remove all of the infested logs from the entire unit before beetles emerge in the spring. (U98). Aside from the case reported above, no studies seem to have been made to determine just what minimum distance of removal is required to prevent reinfestation of the control area.

Submerging the Infested Logs

Hopkins (43) describes this method as "placing the logs in water." Few direct control projects have been undertaken in which it was possible to make use of the submerging method. There are cases where infested trees found on logging operations have been put in the mill pond before sawing, under the assumption that this would destroy the broods. The first attempt to use this as a method on a direct control operation gave some unexpected results which were described by Keen (60 ,page 26).

> "The Arrowhead Lake Company in the summer of 1922 under the direction of J.M. Miller and R.D. Hartman placed a quantity of Ips infested poles, which had been cut in the construction of roads, in the lake to prevent these beetles from escaping and attacking green timber. The poles were later removed and cut into stovewood. The surprising thing encountered in this work was the fact that the beetles were not killed by a submergence of several days or even several weeks.
>
> "Following this experience, Mr. Wagner under the direction of Mr. Miller carried on some experiments at Northfork, California, with the submerging of yellow pine bark infested with the western pine beetle. Sections of bark were submerged in a spring, in water of a constant temperature of 70°F., and a section was removed and examined each week. Two and three weeks' submergence failed to kill any high percentage of the broods and five weeks' submergence was required to bring about 100 percent mortality. As yet no tests have been carried out to determine the efficiency of the method in killing bark beetles in logs placed in mill ponds. It is quite possible that many logs would always float with one side exposed to the air, and that some of the beetles could escape from this portion of the log. It might also require more than five weeks to kill those broods which were submerged."

Converting Logs into Lumber and Burning the Slabs

This is the method most commonly used and on a number of projects the operation has also included hauling the logs for a considerable distance and storing them for a time in a mill pond. A typical operation in which the logs were milled in the woods is described by Keen (65).

> "In the fall of 1928 the Pickering Lumber Company, having contracted to carry on beetle control on a unit of 15,000 acres in Modoc County, California, comprising both the company's and national forest lands, decided to salvage this timber and burn the infested bark at the mill. A sawmill was constructed near the center of the area. The infested trees were located by a survey crew in the usual manner. The trees were felled and then with tractors and fair lead arches equipped with crawler wheels, these trees in full lengths were hauled to the mill. The average distance of haul was about two miles, but some of the trees were brought in for a distance of five miles. About 2,000,000 board feet were salvaged in this manner.
>
> "The cost of this operation compared very favorably with the cost of the old burning method and the treatment was every bit as satisfactory from the standpoint of disposing of the bark beetles. Where the old method would have involved a direct outlay of $4.50 per MBM of timber treated with no return from salvage, the method used cost $6.58 per MBM to bring the trees to the mill, with an estimated value at the mill of $8.00. per M. or a net profit of $1.42 per MBM."

Two other operations by private timber companies to control beetles by logging in northern California and Oregon were described by Keen in this article. He analyzed the economics of the method and concluded that "the salvage method of beetle control can be carried on to good advantage and at a considerable saving over the old methods of control."

Values Salvaged from Infested and Abandoned Trees

The great advantage of control through logging of infested trees over the fell-peel-burn method is the utilization of the material, which may carry all or part of the cost of the control operations. This in large measure depends upon the lumber values that can be realized from the salvaged logs.

The first study of the progress of blue stains and rots in beetle-killed trees was made by Boyce (7), already described under the role of fungi (Section IV ,page 332). Since these beetle-killed trees were cut and left in the woods, Boyce appraised the amount of blue stain and decay following cutting. He concluded that by the end of the second season after attack, the volume of merchantable wood in abandoned trees is so small that it is of little commercial importance.

Patterson (101) describes a salvage control operation in Jackson County, Oregon, during the spring of 1928. Infested trees of the 1927 overwintering generation were logged and milled along with any abandoned trees which contained enough merchantable material for salvage. The latter included trees of the 1927 summer generations and the 1926 overwintering generation. Patterson determined the percent of cull in a series of these salvaged trees. Wood which was only bluestained was not considered as cull since this material, although degraded, could be sawed into boards and sold. Patterson found that:

> "Beetle-killed trees do not deteriorate greatly during the first two seasons (after attack), but after the second season they decay with extreme rapidity, so that by the fourth or fifth season the sapwood is a total loss commercially and the heartwood is badly checked and worm eaten."

Jaenicke (U98) reported a salvage operation at La Pine, Oregon, carried out between June 1 and November 1, 1930, in which 1,200,000 board feet of infested and abandoned ponderosa pines were salvaged from 10,000 acres. The blue stain deduction amounted to 20 percent of the full scale of trees over 22 inches d.b.h. About one-third of the trees were infested, the others abandoned. In another salvage-control operation on the China Hat sale area in the spring of 1936 (U101), 1,127,000 board feet of infested ponderosa pines were cut and logged from 4,120 acres before the beetles emerged. More than 90 percent of the sapwood of these trees was bluestained. This represented 50 percent of the total volume scaled. The effect in beetle control was not reported.

In 1934 and 1935 logging of infested and recently abandoned trees was used in lieu of direct control on two large scale salvage operations in northern California. These operations were stimulated by the epidemic infestations beginning about 1931 which resulted in the accumulation of an immense amount of dead pine in the vicinity of current logging operations. (U280). The companies conducting the two operations were the McCloud River Lumber Company of McCloud, California, and the Fruit Growers Supply Company of Susanville, California. On the latter operation, a complete mill scale study was made by the California Forest and Range Experiment Station to determine the lumber grades that were yielded by the salvaged trees. Both projects were reported upon by Salman and Johnson (U266). Later Johnson (54) published on the results of both the salvage and control phases, and summarized as follows:

> "Nearly 5,000,000 board feet of dead and dying yellow pines were removed from the woods and utilized in nearby sawmills. Entomologists cooperating in the study were interested in determining (1) the relationship between bark beetle development and bluestaining, and (2) the control effect of the salvage operations.
>
> "Infestation patterns made from bole examinations of felled infested trees were used in demonstrating a significant correlation between the bluestaining and the insect species present and between the staining and brood development. Degrade from bluestaining amounted to as high as 50 percent in trees containing advanced broods of *Dendroctonus*, *Ips*, and *Melanophila*.

> "A decline of 40 percent in infestation the year following salvage was noted. Infestations in check areas for the same period remained unchanged or slightly increased. The reduction in loss obtained on the salvage area was approximately the same as that following a direct control project accomplished under very similar conditions on a nearby area."

Bark beetle infestation in 1935 as compared with that in 1934 on salvage, direct control, and check plots

Project Area	Plot No.	Treatment	1935 infestation in percent of 1934 infestation
Shasta	MC-10	Salvage	60.3
	RS-6	Check	100.1
Lassen	L-15	Salvage	61.1
	L-3	Direct control	60.7
	L-1,5,7	Check	108.7

From these and other projects it was found that the one factor above all others which has discouraged the use of logging only infested trees as a control measure is the rapid development of bluestains in the sapwood soon after the tree is attacked. (For discussion of this organism see Section IV, pages 313-316). The amount of degrade found in lumber that is produced from infested or abandoned trees is usually so great that the product cannot compete favorably with the material from sound green trees. This is due mainly to the preference of the trade for unstained lumber, although bluestained boards are still sound and adaptable to many uses; in fact, for interior finish, stained boards have advantages for certain decorative uses. In one case the McCloud Lumber Company found a temporary market for bluestained ponderosa pine salvaged from beetle-killed trees which brought prices equal to their best grades of unstained lumber. It is to be expected that if special uses for bluestained lumber are developed, the values which can be realized from salvaged beetle-killed trees may make such control operations highly profitable.

In the mill scale study described by Johnson (54), the species of infesting insect and the stage of brood development were determined before the logs were put on the saw. The correlation of these data with the amount of bluestain deduction shows the rapidity with which the fungus develops in the sapwood.

Percent of bluestain deduction	Insect Species	Brood Stage
0	*Melanophila californica*	Eggs and small larvae
10	*Dendroctonus californica*	Parent adults, eggs and small larvae
	Dendroctonus jeffreyi	
	Dendroctonus monticolae	
	Ips oregoni	
	Melanophila californica	Large larvae
25	*Dendroctonus brevicomis*	Small and large larvae
	Dendroctonus jeffreyi	
	Dendroctonus monticolae	
	Ips oregoni	
	Melanophila californica	Parent adults,eggs and small larvae
	Ips emarginatus	Prepupal larvae andpupae
50	*Dendroctonus brevicomis*	Large larvae and beyond
	Dendroctonus jeffreyi	
	Dendroctonus monticolae	
	Ips oregoni	Small and large larvae and beyond
	Ips emarginatus	
	Melanophila californica	Pupae and beyond

In 1941 Whiteside (U322) made a study of all the salvage logging projects from which data were available. He reviewed ten reports and published articles, and from these summarized what is known about the merchantability of salvaged beetle-killed lumber. In general, it was shown that if trees are salvaged during the season of attack, most of the lumber is still sound but may run as high as 50 percent degrade because of bluestain; the second year after attack, rots have set in and from 40 to 60 percent of the material must be culled; and for the third year after attack, the cull amounts to about 75 percent, as only the heartwood core of the log is still sound.

SOME RESULTS OF WESTERN PINE BEETLE CONTROL BY DIRECT METHODS

The greater part of the control work that has been carried out against the western pine beetles has employed some direct method of killing the beetles, such as the cut-peel-burn method, or logging, with the primary objective of reducing beetle populations and thus preventing further pine losses.

Direct control methods have been employed over such a long period and on such a vast scale in the western pine region that it is now possible to analyze a number of projects and arrive at some conclusions as to the benefits that were obtained. The amount of work carried on during the period from 1912 to 1952 involved hundreds of separate operations, varying in size from a few acres and a small number of infested trees to the million and a quarter acre southern Oregon-northern California project. Some of these were designated officially as projects and special funds were appropriated for them; many of the smaller operations were considered as routine forest protection jobs and were carried on by contributed labor. During the period of the Civilian Conservation Corps, forest insect control was designated as part of the program of many camps. The greater part of all this work was accomplished by the cut-peel-burn method, supplemented to a limited extent by solar heat and oil treatment of the infested bark. In its over-all effect, this work undoubtedly accomplished the destruction of billions of beetles, but an estimate of the actual saving of timber has been attempted for only a limited number of projects where fairly complete records were maintained. Analyses of these projects are found in a series of manuscript reports which will now be reviewed.

California Region, 1912-1922

In 1922 J.M. Miller prepared a tabulated summary of all bark beetle projects that had been carried out in the California region up to and including the season of 1922. This included 38 separate projects varying widely as to size of area and general infestation conditions. The smallest area listed contained 4,280 acres, the largest 69,400 acres. The majority of these projects were in mixed conifer type in which *D. brevicomis* made up the bulk of the bark beetle population, but with a minor infestation of *D. monticolae* in sugar pine. On about half of the projects follow-up reports included an estimate of the reduction in pine losses by volume comparisons of the seasonal losses for the year preceding and the year following the control work. On at least eight projects these estimates were based on actual check cruises which can be considered reliable (Klamath National Forest, 1912-14; Trinity, 1913-16; and Weed Lumber Company, 1921-23). (98). On the remainder only approximate estimates were made or the results were undetermined.

Total number of projects	388
Total acreage covered	560,430
Total number of trees treated	25,242
Total volume treated	29,015,000 board feet
Total cost of control work	$102,492

Results	Number of projects
Reduction of 50% or more	14
Reduction of less than 50%	3
Satisfactory reduction of losses	8
Temporary reduction of losses	1
Increase following control work (40%)	1
No appraisal of results	11
	38

For the 17 projects reporting reductions by percentage, it was found that the percent of decrease ranged from 40 to 90 percent with an average of 64.5 percent. The general conclusion to be drawn from this summary of the earlier western pine beetle projects is that substantial reductions of losses can be obtained by control work, but the factors that produced satisfactory results in some cases and not in others cannot be readily determined from the available data.

The Southern Oregon-Northern California Project, 1922-24

This project, the largest single undertaking of its kind up to the present time, was planned to control the western pine beetle infestation over an entire timbered subregion of 1,276,000 acres. (57). Practically all of the area included was east-side ponderosa pine type with D. brevicomis predominant in the infestation. The total area was divided into three main theaters of operation, handled by the Forest Service, the Indian Service, and the private owners, respectively; but the entire project was continually under technical supervision by the Bureau of Entomology and Plant Quarantine, and the cut-peel-burn method was applied uniformly and with about the same efficiency throughout the entire project. It can, therefore, be considered an adequate test of control work by this method. From January 1922 to the end of 1924, when the project closed, treatment involved (59):

Total acreage in project	1,276,000
Total acreage treated	393,507
Total number of trees treated	31,512
Total volume treated	35,005,620 board feet
Total cost of control work	$144,880.32

In 1925 Keen (U134) undertook an analytical appraisal of the results accomplished by the project. The basis for this appraisal was far more adequate than for the California projects, which had been carried out by different agencies under widely varying conditions. On the southern Oregon-northern California project the conditions and the methods used were fairly uniform and a large series of check areas were maintained on which the pine losses were accurately measured. These check areas consisted of 29 treated sections (18,560 acres) and 30 untreated sections (19,200 acres).

Keen (U134) determined the results of control work by comparing the annual loss for the years before and after control on the treated sections with that on the untreated sections. This was on the assumption that the natural trend of infestation was the same on both treated and untreated areas and any differences in losses between the two was due to effects of the control work. On this basis he found as an example that between the years of 1922 and 1923 pine losses on the unworked sections decreased on the average of 16.4 percent, while on the worked sections the decrease averaged 43.9 percent; thus he considered that the control work had resulted in a net reduction of 27.4 percent. As an overall appraisal of the benefits of control work on this project, Keen stated:

> "Summarizing the effects of artificial control, we find for the Southern Oregon-Northern California projects -
>
> "1. That the average net effect of control over and above any reduction from natural causes for the past two years has been to cause a 26% and 27% reduction respectively in the losses of the following year.
>
> "2. That the reduction secured varied with the intensity of the infestation. With a loss of less than 65 trees per section (100 board feet per acre) the effect of control was often totally obscured by the operation of natural factors. Above 65 trees per section reductions increased as the intensity of infestation increased. With losses of 250 trees per section (400 board feet per acre), 48% reductions were secured by control.
>
> "3. That subsequent infestation depended to a considerable extent upon the amount of infestation left on the area.
>
> "4. When not obscured by the effect of other factors, the reductions secured were directly proportional to the amount treated and that in general for every tree treated approximately one less tree was killed the following year."

Keen also recognized differences in the results secured according to the time of year when the work was done.

> "From the results on the check sections as listed previously, we have the following comparison of the effect of spring and fall work:
> Spring work 1922 - 60 trees saved for every 100 trees treated.
> Spring work 1923 - 60 trees saved for every 100 trees treated.
> Fall work 1922 - 113 trees saved for every 100 trees treated."

Thus the results of the fall work show up much better than those from spring work, especially the late spring work. The probable reasons for this are as follows:

> "1. The beetles in bark on felled trees which escaped the burning were either killed to some extent by molds and excessive moisture, or where the bark was on top of the logs or scattered on the ground by the heat of the sun late in the spring before emergence.
>
> "2. The beetles in standing trees which escaped the treaters were to a large degree sought out and eaten by woodpeckers during the winter when woodpeckers were forced to concentrate on the small number of missed trees for their food supply.
>
> "3. The odor of fresh cutting and burning was absorbed by the winter snows so that by the time of flight the attractive influence of the slash and the burning was negligible; thus avoiding any concentration of flying beetles into the treated area."

The results of this project also indicated that little could be gained by working an area over again the year following the initial control work.

> "Summarizing the results of nine check sections treated in the spring of 1922, we find that following control the loss of 1921 was reduced from 1,165 trees to 815 trees, or a reduction of 31 percent. The next year the loss was reduced to 695 trees. This, however, is a reduction of 15 percent, while the natural reduction on all worked units averaged 16 percent. Therefore, following the first work the units responded to the general decrease for the region.
>
> "Thus there was no additional reduction due to control but the reduction which had been secured was simply maintained and the units otherwise responded to the natural factors which became operative."

Modoc Control Projects, 1931-32

The results from two fairly large control projects carried out within the Modoc National Forest during the winter and spring of 1932 against sharply increasing infestations were appraised by Salman (U257) two years after the work was completed. The control phases of the two projects compare as follows:

	Badger Project	White Horse Project
Period of control work	12/31 - 4/32	12/31 - 4/32
Total acreage treated	19,680	12,140
Number trees treated	1,932	1,027
Volume treated MBM	2,345	1,454
Cost of project	$9,478	$3,243

Salman's appraisal of the effects of the control work is quoted in entirety:

> "It has been assumed that if no treatment had been done, the treated plots would have shown the same general trends as the untreated plots in the near vicinity. The following table gives the results of the cruises in terms of volume, percent of the 1931 infestation, and probable savings resulting from the control operations.

"Badger Control Project

	1931	1932	1933(est.)
Average for 4 treated plots			
Loss per acre, BM	243	229	144
Percent of 1931 loss		94.2	59.3
Average for 3 untreated plots			
Loss per acre BM	251	392	258
Percent of 1931 loss		156.2	102.8
Theoretical losses without control		380	250
Savings from control			
BM per acre		151	108
MBM on project area		2,972	2,086

Total two-year period, project area - BM	5,057,760
Stumpage value	$15,173
Cost of project	$9,478
Savings above cost	$5,695

"White Horse Project

	1931	1932	1933(est.)
Average for treated plot			
Loss per acre, BM	192	111	144
Percent of 1931 loss		57.8	75.0
Average for untreated plot			
Loss per acre, BM	313	487	147
Percent of 1931 loss		228.6	69.0
Theoretical loss without control			
BM per acre		439	132
Savings from control			
BM per acre		328	-12
MBM on project area		3,982	-146

Net savings, two year period	
BM on entire project area	3,836,240
Stumpage value	$11,508.
Cost of project	$3,242.83
Savings above cost	$8,266.

"Although it is believed the plot results for the Badger project represent above average conditions, the plot comparisons for the White Horse area are not considered as satisfactory. It is probable that the actual savings are below those indicated above, but qualitative observations on the area would indicate a considerable benefit derived from the control work.

"Summary

"1. The control projects of 1931-32 in the Modoc National Forest were directed against a rising epidemic and took place during the first stage of the epidemic cycle.

"2. The major effect of the two control projects, which in all projects appear in the year immediately following control, have been secured by cruises of actual losses on selected plots.

"3. These cruises show that on the Badger control project area treated plot infestations decreased 5.8 percent in the year following control, while untreated plots showed an increase of 56.2 percent, a difference of 62 percent in favor of treatment. In the White Horse project area, treated plot losses dropped 42.8 percent and untreated plot losses increased 128.6 percent, a net difference of 170.8 percent in favor of treating.

"4. Further favorable differential between treated and untreated plot losses occurred in the Badger area during the second season after treatment. Unfavorable differential occurred in the White Horse area in the second season, although it is believed the situation in 1933 represented a nearly normal condition.

"5. The results show the benefit derived from treating an epidemic in its first stages and when compared with results following the 1928-29 control which was directed against a decreasing infestation show the superiority of combating increasing epidemic infestations as a means of saving values."

Willow Springs and Badger Control Projects, 1934

These two projects were carried out in the eastside pine type of northeastern California during the winter and spring period of 1933-34. The two areas were quite similar as to infestation types and general stand conditions, and the timing of control work and methods used were the same. The results, however, were quite divergent and illustrate the erratic response of western pine beetle infestations to the effects of control work.

In 1936 Salman (U268) compared the results obtained from these two projects. The data on which the appraisal was made consisted of accurate cruises of the annual loss on five treated plots (16,000 acres) and 13 untreated plots (4,160 acres).

	Willow Springs project	Badger project
Period of control work	12/33 - 5/34	12/33 - 5/34
Acreage covered	23,250	41,345
Number of trees treated	4,155	5,848
Volume treated	3,949,000 b.f.	5,622,640 b.f.
Cost of control	$18,966.70	$29,487.14
Results on control area		
1st year after control	22.9% decrease	121.3% increase
2nd year after control	53.6% decrease	29.0% increase
Infestations on check areas		
1st year after control	72.3% increase	94.9% increase
2nd year after control	21.1% increase	115.7% increase

Although the areas were worked for one year only, Salman apparently figured that the effects of control extended over two years. The fact that, during the second year after control, losses on the Badger control area increased 29 percent while those on the check areas increased 115.8 percent is the only favorable result which can be attributed to this project. By applying this to the entire project area, Salman figured that 4,270,700 board feet of timber was saved as a result of control work on the Badger area.

The results on the Willow Creek project were clear-cut and showed a definite profit on the control work. On this area the volume of timber that was saved, according to the difference in losses between the control and the check areas, was figured to be 10,500,000 board feet.

In attempting to explain the widely divergent results obtained from these two projects, Salman made the following comments:

> "In both areas the infestations were increasing in 1933. In both the cycle reached its peak. Both included fringe areas and apparently similar environmental conditions. Composition of infestation was more mixed in the Lassen (Willow Creek) than in the Modoc (Badger) area, although in both areas species other than the western pine beetle were markedly active. Both areas were large,both bounded by timber on south, southwest and east. Both were exposed to heavily infested timber within 20 miles on west and adjacent on east. Infestations were lighter to the south.
>
> "We cannot put our finger on any particular factor responsible for the difference. It is possible that the lightly infested sparse stand south of the Willow Springs Project was a better barrier than on the Modoc.It is possible that the continued attrition of environmental factors,or flathead borers or other insects,had reduced the level of resistance in the Modoc stands to a point much lower than on the Lassen."

California Region, 1931-36

During this period high epidemic losses occurred in both the eastside and westside pine types and a large amount of control work was carried on by federal and private agencies on national forest and national park areas. The majority of the projects were financed through CCC and other emergency funds. The total program carried on during the period consisted of 41 separate projects, which covered a total of 560,000 acres at a cost of $327,000. Although most of this work was under the technical direction of the Bureau of Entomology and Plant Quarantine, administration of the control work and immediate field supervision were provided by the agencies conducting the projects.

Salman (U268) attempted to make an appraisal of the results of this series of projects. Detailed data from annual loss cruises were available for a few areas only so that the entire program could be appraised only in a general way. Salman first reviewed the projects according to the types of areas which were listed by Craighead et al. (26) as representing the different conditions under which direct control work was considered to be entomologically sound.

Type of area	Number of projects
1. Recreational areas	
a. Small, well isolated areas	4
b. Areas with well defined boundaries	10
2. Commercial timber stands	
a. Eastside pine stands	12
b. Westside mixed conifer stands	15
Total	41

Salman compared Craighead's (26) conclusions concerning the results of direct control with the apparent overall results obtained on these projects. He quoted the following from Craighead:

> "One season of thorough control work results in a reduction of western pine beetle losses on the treated areas as compared with similar untreated areas.
>
> "The benefits have been greatest when the natural tendency of the infestation was upward.
>
> "Under a declining infestation there was only a small difference in favor of the treated over the untreated areas.
>
> "The benefits of control work have been temporary, lasting only one or two seasons, and a return to conditions similar to those on untreated areas can be expected unless work is continued on the same area year after year."

Insofar as he was able to determine the results of western pine beetle control work from 1931-36, Salman summarized his conclusions as follows:

> "On the whole, it can be said that Craighead's general conclusions concerning the results of direct methods of forest insect control have been substantiated by recent experience. In addition, it may be stated that control of infestations at the peak of an infestation cycle results in little or no saving of timber. However, the degree of control that is secured by one season's work against increasing or decreasing infestations is not always satisfactory. The fact that results are temporary and the limitation imposed by the economics of control under the present policy, all make it imperative that more consistently effective, more permanent and cheaper methods of forest insect control be secured."

Warm Springs Indian Reservation, Oregon, 1932-40

In 1940 Weaver (U310) made a survey of the Warm Springs Indian Reservation to evaluate the results obtained from seven consecutive seasons of western pine beetle control which was carried on prior to and including the 1940 season. This appraisal covered a total of 57,731 infested ponderosa pines with a volume of 37,149,000 board feet, treated on 320,000 acres at a cost of $266,434.79. All of this work was carried on during the winter control seasons by the cut-peel-burn method. The acreage figure includes the reworking of some areas which were covered more than once.

Weaver analyzed the results of the work by a series of statistical tables, based largely on annual loss cruises of 19 check sections, totaling 11,767 acres in both treated and untreated areas. His general appraisal of the effects of control was based on what the predicted loss would be if no control work had been done and was stated as follows:

> "Pine beetle control work conducted on the Warm Springs Reservation during the past seven years has resulted in the saving of 131 million board feet of ponderosa pine. At the rate of $3 per M board feet the control work conducted has thus resulted in the saving of $393,000 in stumpage values. To effect this saving, $266,434.79 of I.E.C.W. and CCC I.D. funds have been expended."

Weaver also brings out the point that the effects of control were most marked during those years when the total area of heavy infestation was adequately covered by the work. This he illustrated by means of a graph and by the following discussion:

> "... The peel and burn control work has profoundly influenced the course of the beetle epidemic on the Warm Springs Reservation... However, the beneficial effects of the control work are always temporary and the tendency is for the infestation to resume its normal course. During the years 1934, 1935 and 1936 ample funds were available and almost all of the epidemically infested portions of the reservation were covered by control work. Subsequent to that date, however, the amount of funds available for such work has steadily declined, while at the same time the beetles have been on the natural increase."

FACTORS INVOLVED IN CONTROL PLANNING, STRATEGY, AND POLICY

Quite often the decisions that are required in recommending, planning, and executing bark beetle control projects are concerned with questions of policy and strategy as well as technical knowledge of the beetle and of control methods. Control planning involves such questions as: How large an area should be included in the control unit to insure protection from outside infestation? How intensively should the area be covered by eradication work? Under what conditions is control warranted? The answers to many of these questions must be found in deductions drawn from experience with control operations rather than from biological studies. However, a number of studies have been made of certain problems that affect control planning and policies and these will be reviewed in this section.

Methods of direct control are based on the thesis that dead beetles kill no trees, and their use is designed to accomplish control by rapid reduction of beetle populations. Although the methods themselves are fairly elementary and simple, their success usually depends upon an understanding of the principles involved in when, where, and under what conditions control should be undertaken. Control projects require strategic planning to get the best results, like any other undertaking that requires counter action against an aggressive enemy.

Hopkins (43) discussed these problems of strategy and first laid down the principle that attempts to exterminate the beetle are unnecessary.

> "It must be kept in mind that beetles must occur in great numbers in order to be successful in their attack on healthy trees. If their number is reduced and kept below that required for killing trees they can do no harm. Therefore in the case of a destructive outbreak, it is necessary to destroy only from 50 to 75 percent of the beetles in order to bring them under complete control."

This original policy statement of Hopkins later became known as the percentage principle of control and aroused a controversy which will be discussed later. Under the topics of "Requisites for successful control," "How to check and control an extensive invasion," "How to control a limited attack," and "How to maintain control," Hopkins (43) discussed further the general principles underlying direct control policy. However, these statements made in Bulletin 83 apply to Dendroctonus beetles as a group rather than specifically to any one species. It should also be kept in mind that at the time Bulletin 83 was published, no western pine beetle control projects had been undertaken, so that Dr. Hopkins' ideas of control strategy must necessarily have been based on his knowledge of the habits and behavior of the beetles, and not on experience with actual control.

Some of the questions of basic control policy and procedures appear to be of far greater importance than others, but all must be taken into account if control work is to be undertaken on a sound basis. Those that apply to the immediate planning of a project will be considered first.

Boundaries of the Control Area

It is essential that the size and boundaries of a control area be settled upon before intelligent planning can be done. The selection of boundaries may be regulated by a number of considerations, the most important being the extent and distribution of the epidemic infestation that should be brought under control. However, quite often a large area of infestation can be broken down into smaller units which can be worked independently and these may be blocked according to cooperating ownership, topography, and type barriers. Usually the boundaries are determined by the combination of a number of factors. The paramount purpose, however, is to select an area where the results of the first season of control work will not be upset by an influx of beetles coming in from outside areas that have not been treated.

The ideal control area is a satisfactory infestation unit such as that described under surveys in Section V, pages 547-550 In general practice, control areas selected usually have conformed to one of the following three types:

(1) Small, localized infestation centers which contain the only serious infestation within a much larger forest area.

(2) Areas containing a widely distributed infestation, but which are well isolated from other bodies of infested timber by topographic barriers or breaks in type or both.

(3) Areas without satisfactory boundaries of topography, type barriers, or breaks in the distribution of infestation, but which are considered to be so large in extent that the control results will not be quantitatively affected by beetles which infiltrate from outside adjacent areas.

The problems of selecting satisfactory boundaries for control units are most frequently encountered under the type of area designated under (3). For this reason a great deal of study has been given to the flight habits of beetles, and to the character of the reinfestation developing along the boundaries of control areas which are exposed to adjacent infested areas.

In 1925 Keen (U134) made an analysis of the data from the southern Oregon-northern California control project to determine how much the infestation within the controlled area had been affected by adjacent untreated areas. Most of these data came from the Owens unit where no satisfactory natural boundaries could be found and ownership lines had been used instead. The control work had been extended up to section lines in continuous pine type leaving similar sections untreated immediately adjacent.

Keen (U134) found that:

> "Only on the edge of the area and within the first mile did the infestation show an increase when adjacent to untreated sections. This would suggest that after two periods of flight the adjacent infestation had only drifted back into the area for one mile."

Similar records on this zone of control influence were obtained by Patterson (U213) in 1925. The Long-Bell Lumber Company carried on control work during the spring and summer of that year on its tract on the Klamath Indian Reservation. The control area consisted of a block of 26,000 acres which was a part of a much larger area of infestation. Natural control boundaries were found for three sides of the tract, but the remaining side consisted of a township line with heavy infestation in pine type outside the boundary. The Company covered the tract with cut-peel-burn control during the spring period and followed this with summer maintenance work, particularly along the exposed boundary. In summarizing the results, Patterson reported:

> "It was fully expected that the beetles from the untreated outside area would reinfest the treated stands along the exposed border. This occurred to some extent during the flight periods which followed the spring control work, although the amount of this reinfestation was far less than expected. The invasion was limited to a strip of forest one-half mile wide which lay along the border. An attempt was made to combat this during the summer and fall work by treating the trees attacked as soon as they were discovered. Many of the trees in the fall work were located along this strip and their treatment undoubtedly prevented further spread into the area. An interesting feature of the encroachment of the infestation along this border into the controlled area was the rate of its advance which was gradual and progressive. It did not advance further than one-half mile during the season."

On the San Joaquin project from 1920-24 special efforts were made to determine the width of the zone within which the volume of infestation on a treated area is affected by beetles coming in from adjacent untreated areas. In summarizing the results of the San Joaquin project, Miller (U186) reported that on the Forked Meadow unit, which was worked intensively in an attempt to exterminate the beetles, "practically all infested trees that developed in this unit during the 1924 season could be accounted for by beetles coming from infested trees not over one mile distant." This extermination unit was exposed on one side to an untreated area without a natural barrier.

These records and other observations have all served to support the idea that a buffer zone of about one mile is necessary for the protection of a control area where natural boundaries are lacking. It is obvious that an area of four sections, two miles square and surrounded by untreated areas, is too small for a control unit because any part of the area would be within one mile of the boundary. However, a square area of 16 sections would have four sections or 25 percent of the control area in the center which would be protected by a buffer zone one mile wide; or a township with 36 sections would have 16 sections or about 45 percent of the control area so protected. Circular areas would of course increase the percentage of protected areas in proportion to the one mile zone around the perimeter. Consequently, where no natural boundaries are available, it would be necessary to select larger areas of several townships in order to have a control unit that would not be subject to serious reinfestation coming in from surrounding untreated areas.

In actual practice, however, the boundaries of control units have usually been determined by a combination of factors, and the areas selected have shown extreme variation in size. From an administrative viewpoint, the best size for a control unit is an area which can be covered in one control season by a camp of about 25 men; and in the average run of western pine beetle infestations this has involved from 10,000 to 20,000 acres of pine type. Most desirable of all is a unit of about this size which consists of a natural basin or water shed drainage where the work can be started at lower elevations early in the season and carried into higher elevations as the season advances.

Selection of Control Methods

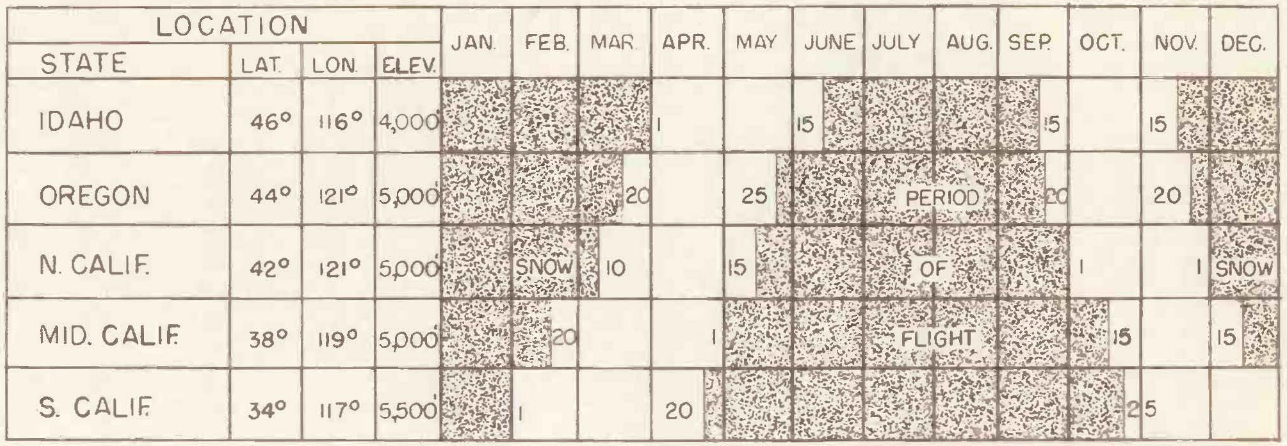
Decision as to the method of direct control that is to be used must be governed by the conditions of the area, available labor, equipment, and the seasonal timing of the control operation. Under high fire hazards, the cut-peel-burn method must be modified to meet safety requirements or else solar heat, oil treatment, or other methods substituted. Otherwise the control work must be closed down. From a practical standpoint, the selection of the method to be used must be left to the judgment of those responsible for the planning and supervision of a project. No special studies have been made or reports issued that will serve as a guide to these important decisions.

Seasonal Timing of Control Work

The seasonal period when control can be carried on to the best advantage is dependent upon the factors of latitude, elevation, and climatic variations which influence the flight periods and the dormant periods of the beetles, and such factors as affect the accessibility and working conditions of control areas. Western pine beetle broods can be destroyed any time of the year that infested trees can be found by using methods suited to the season and conditions of the area, such as cut-peel-burn in winter and solar heat in summer. However, the clean-up of all infested trees within any large area can best be accomplished by cut-peel-burn during the dormant overwintering period. Keen (60) has summarized in chart form the regional differences in periods when control on overwintering broods can be carried on to best advantage. (Figure ~~60~~ 65).

Figure ~~60~~ 65.— Open seasons for western pine beetle control, in ponderosa and Coulter pine.

(Page 651a follows)



LOCATION				JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEP.	OCT.	NOV.	DEC.
STATE	LAT.	LON.	ELEV.												
IDAHO	46°	116°	4,000'	▨	▨	▨	1		15 ▨	▨	▨	▨ 15		15 ▨	▨
OREGON	44°	121°	5,000'	▨	▨	▨ 20		25 ▨	▨	▨ PERIOD	▨	▨ 20		20 ▨	▨
N. CALIF.	42°	121°	5,000'	▨	▨ SNOW	▨ 10		15 ▨	▨	▨ OF	▨	▨	1	1	▨ SNOW
MID. CALIF.	38°	119°	5,000'	▨	▨ 20		1	▨	▨	▨ FLIGHT	▨	▨	▨ 15		15 ▨
S. CALIF.	34°	117°	5,500'	▨	1		20 ▨	▨	▨	▨	▨	▨	▨ 25		

Figure 65.-- Open seasons for western pine beetle control in ponderosa and Coulter pine.

Keen also lists the advantages and disadvantages to be expected in control work during each of the fall, winter, spring, and summer working periods in the following table.

Fall Control

Advantages	Disadvantages
1. Destroys beetles in early stages before any emergence has occurred.	1. Trees difficult to find.
2. Some predators may escape destruction.	2. Bark hard to peel.
3. Fires progressively easier to control.	3. Shorter working season.
4. Easy transportation into camps over firm roads.	4. Camp may get caught in snow-storm,making it difficult to get out.

Winter Control

1. Destroys beetles before any emergency has occurred.	1. Trees difficult to spot. 2. Bark hard to peel.
2. Permits covering larger area with seasonal work.	3. Trees difficult to burn. 4. Transportation difficult.
3. No danger from fires escaping.	5. Work interrupted by storms.
	6. Usually expensive.

Spring Control

Advantages	Disadvantages
1. Longer working period.	1. Many beetles escape through early flight.
2. Trees easy to spot.	2. Work may be cut short by advent of dry hot weather.
3. Trees easy to peel.	3. Fires progressively more difficult to control.
4. Trees easy to burn.	4. Ground soft and early transportation of camps difficult.

Summer Control

Advantages	Disadvantages
1. Permits treating additional area or doing clean-up work on special projects.	1. Has failed to give satisfactory results.
	2. Dangers from fires great.
	3. Solar heat method not always effective.
	4. Beetles in flight and only small percentage destroyed.
	5. Usually expensive.
	6. High percentage of predators destroyed.

Types of Infested Trees Selected for Treatment

The bark beetle population to be found on any control area is rarely made up of pure broods of the western pine beetle occupying all of the available bark surface of every infested tree. The infestation more often is mixed with that of Ips, flatheads, or the mountain pine beetle in various combinations. Also, the broods of the western pine beetle are seldom found in a uniform stage of development. For overwintering populations, the bulk of the broods will be in the more advanced larval stages, but some infested trees will contain only the first stage of attack with parent adults and eggs in the phloem area, while at the same time other trees will be partially abandoned with only a few new adults remaining to comprise the straggling emergence of the main brood. Still further complications are set up when topkilled trees are prevalent in an area which have only a small part of the upper bole infested. All trees of the above types must be classed as infested since they contain some beetle populations.

Before setting up instructions for the spotting and treatment of trees on any control project, a decision must be reached whether all types of infested trees are to be included or a selection made of the more heavily infested trees. From the standpoint of killing the most beetles for the time and effort expended, it is often possible to accomplish more by concentrating the work on trees with the heavy broods and leave untreated those that are only lightly infested.

The practices of selecting trees for treatment have varied with conditions in the different control projects. For the most part the trees that were selected have been defined by instructions issued to the spotters. Apparently, the practices that have been followed in the different projects were not arrived at through the results of adequate studies or tests of methods, but for the most part have been based on the experience and best judgment of entomologists connected with the projects.

In the original control projects there was little selection of infested trees for treatment. Perhaps one reason for this was that the cutting and peeling of all infested trees gave a fairly complete picture of the total infestation on an area, and the data thus obtained had a great deal of value in analyzing the entomological factors. Hopping (48) in his control manual issued in 1914 specified treatment of "100 percent of the infested trees," which left little latitude for selection. The "Manual of Bark Beetle Control" by Keen (60) issued in 1927 recognized the advantages of selective treatment and specified:

> "Only trees with well developed broods of beetles should be marked for treatment and these before the trees have been two-thirds abandoned. In case of doubt as to whether or not the tree is heavily infested or has been partly abandoned, and a decision cannot be reached after a reasonable amount of inspection, a good rule is to mark the tree for treatment."

Instructions that have been issued to spotters and treaters on some projects have been much more detailed and specific than the above statement. For the large southern Oregon-northern California project the instructions prepared by Keen (U131) included the following classification:

> "If on chopping into the bark, it is found that the tree is dead or dying, a careful examination should be made to find if it contains live bark beetle broods.
>
> "Trees to be marked for treatment are those over 12" in diameter.
>
> "1. Containing live broods of the western pine beetle or the mountain pine beetle in the stage of larvae, pupae, or new adults (not more than 70 percent emerged) located within the project area and accessible to camps.
>
> "2. Windfalls containing live broods of the above beetles.
>
> "Trees not to be marked for treatment are those
>
> "1. Under 12" in diameter (unless in a group)
>
> "2. Showing only doubtful evidence of the western pine beetle or mountain pine beetle.
>
> "3. Partially attacked trees or those containing broods only in the egg stage, or from which broods have completely or for the most part emerged (over 70 percent).
>
> "4. Trees abandoned in the top and infested for less than one log length at the base, or only on one side at the base.
>
> "5. Very remote from control operations so that their treatment would be excessively expensive.
>
> "6. Trees infested only with Ips beetles or flatheads."

In the westside type of the Sierra National Forest in 1931-32, a different set of rules was used for the selection of trees to be treated. Here the problem was complicated by a very active Ips confusus infestation which had initiated the first attack in the tops of a high percent of the infested trees, followed later by western pine beetle attack in the lower bole. Gustafson (U73), who was in charge of the project for the Forest Service, used the following rules which were drawn up by the Bureau of Entomology and Plant Quarantine.

I. Trees to be marked for treatment

1. Good western pine beetle brood at base regardless of color phase of the foliage.

2. Green base, but with entire or most of crown fading, indicating that tree will die in any case.

3. Green base with foliage green or partially fading, but with pitch tubes or woodpecker work indicating western pine beetle attack in upper bole.

4. Infested trees partially abandoned by the western pine beetle, but with more than 25 percent of brood remaining in the bark.

5. Sugar pines infested by the mountain pine beetle where these occur in the ponderosa pine type.

II. Infested or faded trees not marked for treatment

1. Top-killed trees with less than 50 percent of crown faded and showing no indication of western pine beetle attack on the bole; these trees represent distinct top-killing by *Ips*.
2. Western pine beetle infested trees from which the greater part of the brood has emerged (less than 25 percent remaining in the bark).
3. Trees infested only by flathead at the base.

Differences in the instructions issued for these two projects can be explained by widely different conditions in the two areas and the types of infestation. The southern Oregon-northern California project was located in eastside pine type with the only serious infestations made up of the western pine and mountain pine beetles. The control effort was first directed toward destroying as much as possible of the population during the limited control period; consequently, the instructions were drawn so as to avoid dissipation of this effort in the treatment of doubtful or partially infested trees, *Ips*, and flathead infestations, and infested trees located in remote parts of the control area.

The Sierra project, on the other hand, was characterized by a top-killing Ips epidemic, which at the time of the control work was being followed by a build-up of western pine beetle in the top-killed trees. It was anticipated that the Ips infestation would soon die out; the control effort, therefore, was directed toward destroying as high a percent as possible of the western pine beetle broods in order to prevent further momentum of this infestation in the weakened top-killed trees which had survived the Ips attack. Consequently, all trees containing western pine beetle broods were treated except those that were nearly abandoned. Ips infestations were not treated except when the broods occurred in trees infested by the western pine beetle. This strategy proved successful since the Ips infestation disappeared the following year, and the western pine beetle was brought under control by the cut-peel-burn treatment.

Hard and fast rules cannot be applied strictly to the selection of trees to be treated, but must often be modified to meet special conditions in different areas, forest types, and regions. However, the entomological considerations involved in selecting trees infested by the western pine beetle and its associated insects are discussed in the following summary:

Western Pine Beetle

Heavy advanced broods in the bark

Trees are always treated when more than half of the bark surface is infested.

New attacks - parent adults and eggs in phloem area.

These trees have been treated on nearly all projects, although peeling and burning is difficult and the number of insects destroyed is small compared to trees with larval broods. However, if freshly attacked trees are left untreated, they are capable of developing strong broods to reinfest the area.

Partially abandoned trees.

These are usually left untreated if 75 percent or more of the broods has emerged. Even when the emergence is less than this, their treatment is of questionable value because these partially abandoned trees carry a very high percent of the insect predator population.

Associated Insects

Ips confusus and _Ips oregoni_

No special attention has been given to the treatment of _Ips_ infestations when these appear to be a minor or secondary factor in the total infestation. However, whenever _Ips_ trees or _Ips_-infested tops could be "thrown-in" with the treatment of western pine beetle trees without an undue amount of extra work, they have been included in the treatment. When _Ips_ has been an aggressive factor in the total infestation, groups of infested poles and single trees have been treated. Trees infested only by _Ips_ in the tops will be discussed under "top-kills."

The mountain pine beetle.

The mountain pine beetle in ponderosa pine has been a minor factor in western pine beetle infestations. It is usually treated, however, because it occurs in the same general bole areas as D. brevicomis and little extra effort is required to treat it. Sugar pines infested by the mountain pine beetle are fairly common in westside mixed type where practically all control projects have followed the practice of treating infested sugar pines found in the same areas with D.b. in ponderosa pine.

Pine flathead (Melanophila californica).

In some areas flathead trees have been treated because they compose a high percent of the total infestation and are causing serious losses. This has been especially true for certain projects in southern California. For the most part flathead infestations have been treated only when they occur in the same trees with the western pine beetle and no extra work is required to dispose of them.

Top-killed trees.

The question of what to do about top-killed trees has always been a difficult one for the spotter and treater to decide. The green base where the spotter makes his examination of the bark gives no indication whether the top was killed by Ips, flatheads, or Dendroctonus; also there is nothing but the color of the foliage in the dead top to indicate whether the tops are still infested or have become abandoned.

The rules for treating top-kills have been influenced by the fact that about 50 percent of recently top-killed ponderosa pine are attacked on the main bole by the western pine beetle within a few years, but the remaining 50 percent may survive for long periods as stag-topped trees. Falling a top-killed tree for direct control involves the waste of lumber in the green part of the main bole in order to treat a small amount of infestation in the top; it also involves the risk of finding an abandoned top when the tree is felled. Consequently, the tendency on most projects has been to favor the leaving of top-killed trees on the chance that they will survive.

The general rule that has been followed is the one adopted on the Sierra project - that is to leave untreated top-killed trees which have less than 50 percent of the crown faded, unless there are evident signs to indicate that new attacks are advancing below the top-killed portion. If more than 50 percent of the crown has faded and there are good signs that the dead part of the bole contains good broods of D.b., the tree is felled and treated.

The Percent of Infestation to be Treated

The intensity with which a control area is to be covered to find and treat infested trees directly affects the cost of the work and is, therefore, one of the first elements to consider in control planning.

On the first western pine beetle projects that were undertaken by the Forest Service, some misunderstanding developed regarding application of the percentage principle as advocated by Dr. Hopkins. It was apparently assumed that 75 percent control meant that 25 percent of the infested trees that had been located on an area should be deliberately left untreated. Hopkins' explanation of the practice was stated (n.43) as follows:

> "The force should be directed to removing as large a percentage as possible of the infested bark from standing infested trees or from those felled for that purpose. The first work should be done in the principal areas and larger patches. The work should be planned and executed with the object of destroying the greatest possible number of broods for the time and labor involved; that is, if there are more infested trees than can be barked within the specified time and 5 or 6 times as many insects can be killed by removing half of the infested bark from 3 or 4 trees as could be done in the same time by removing all of the infested bark from 1 tree, the former procedure is far preferable."

Hopkins' reasoning in advocating the leaving of some infestation in a control area seems to have been that 100 percent treatment would destroy all the beneficial insects as well as the bark beetles; so that the beetles coming in from the outside to reinfest the control area would find conditions quite favorable for a rapid increase of their numbers. Therefore, some of the infestation should be left untreated either intentionally or otherwise in order to preserve enough beneficial insects to maintain the natural balance.

Ralph Hopping of the Forest Service made a very different interpretation of percentage control. In a mimeographed manual which was issued by the Forest Service, Hopping (48) stated that in planning bark beetle control work, "the aim will be to treat 100 percent of the infested trees." In the same manual Hopping stated his belief that "bark beetles do not fly any great distance if trees of the species required by them are nearby." According to this reasoning if 100 percent eradication is accomplished in a control area, the beetle population would be eliminated for a long time to come.

The first western pine beetle control projects developed results which indicated that the difference between treating 75 or 100 percent of the infestation for the first year of control work was largely an academic issue. No matter how intensively the spotting and treating were done, it was found when subsequent checks were made that some infestation always escaped. Even with the most careful and thorough work, it was difficult to find and treat much more than 75 percent of the total infestation. This was mainly due to failure to find broods concealed in trees that had not faded color when the area was spotted, in windfalls, and in the mid-bole of top-killed trees. Because of this concealed infestation, both the Forest Service and the Bureau of Entomology and Plant Quarantine soon adopted the practice of treating all the infested trees that could be found; it was considered that enough infestation would be missed anyway to take care of the percentage principle of control.

In checking the percentage of infested trees spotted at different seasons of the year, Keen (U132) found on the southern Oregon-northern California pine beetle control project 63 percent of the summer generation was found by spotters in summer control work; 76 percent of overwintering infestation was found in fall control work; 80 percent was found in winter control spotting; and 85 percent in spring spotting. During the subsequent summer's survey 88 percent of the previous year's loss could be spotted. This showed that with the usual three-man spotting crew about 12 percent of the infestation was inevitably missed. Keen also found no positive correlation between the percent of infestation treated on sections, when between 30 and 75 percent of the infestation was treated, and the subsequent reinfestation.

Recleaning of Control Areas

Although this factor of concealed infestation largely liquidated the issue over percentage control, the controversy continued over the necessity for recleaning, i.e., the treatment of an area during the second and third years in order to eradicate infestation that was missed during the first year of control. On most projects a reinfestation of from 25 to 50 percent of the original volume developed the second year. According to Dr. Hopkins it was unnecessary to reclean an area after the initial control work had broken the force of the epidemic, because natural factors could be expected to take care of the infestation that was left over. Hopping (48) disagreed with this in his control manual:

> "On the Barkhouse project of the Klamath National Forest, only 86.7 percent of the infested trees were cut and burned in 1912. The infestation is now nearly or quite as bad as the original infestation before the initial control. Control work once begun must be followed up for at least three years to be effective and after that must be followed by the regular administrative force and occasional trees cut and burned."

The first two western pine beetle control projects initiated in 1912 by the Forest Service on the Klamath National Forest are historically important because they represent the first effort to arrive at an understanding of the issues involved in the application of percentage control. The Craggy Mountain and Barkhouse units in the Klamath River watershed, containing about 15,000 and 20,000 acres respectively, were covered by cut-peel-burn control work in the spring of 1912. Because these were among the first attempts at western pine beetle control, the projects were regarded as partly experimental, and for this reason, the Bureau of Entomology took the responsibility for spotting of infested trees and supervision of control methods. The policy followed on this initial work was to treat all of the 1911 overwintering infested trees that could be found during the control period. Later in the season, Hopping checked the Barkhouse unit and found that 87.6 percent of the overwintering infestation had been treated, the remainder having been overlooked by the treating crews. It was estimated that a similar percentage had been treated on the Craggy Mountain unit.

Following this initial control, a considerable amount of reinfestation developed on both units during the 1912 season. By fall, it was found that the 1912 overwintering infestation would be about 40 percent of the 1911 overwintering, or a reduction of about 60 percent in the volume of infestation which could be attributed to the first year's control work. It was decided then to reclean the Craggy Mountain unit and leave the Barkhouse untreated. This program was carried out in the spring of 1913; and no further control work was done on either area during succeeding years, but periodic surveys were made to determine the amount of infestation which developed annually up to the close of the 1916 season.

In April of 1914, Chief Forester Graves and other representatives of the Forest Service met with H.E. Burke and W.E. Glendenning of the Bureau of Entomology to make an inspection of the areas to see what results had been up to that time. The obvious condition was that during 1913 there had been a marked decline in the infestation (later determined to be about 45 percent) on the Craggy unit after it had been recleaned; while on the Barkhouse unit, which had not been recleaned, the decline had been even greater (later found to be about 65 percent). It was also obvious that the infestation had been reduced in both units to an endemic, non-aggressive condition and was causing no serious timber losses. The same endemic conditions were noted in the adjoining check area of McKinney Creek, which had not been treated by any control work.

Therefore, the results up to April 1914 appeared to give ample support to the percentage principle as advocated by Dr. Hopkins, and the Forester prepared a statement to be attached to Hopping's control manual for the purpose of reconciling opposing viewpoints that had previously been held by the two Bureaus. After reviewing the conflicting interpretations that had been made of percentage control, the Forester concluded:

> "The first aim of control is to attack the points of concentration, striking the insects where they are most numerous. Because of the relationship between different parts of the infestation units, the destruction of large broods at concentrated points affects the rest of the infestation; and when the reduction of the insects in number has been carried to a certain point, the backbone of the infestation is broken and the insect attacks become scattered... This policy seems to be justified by the results on the Klamath Forest."

This conclusion held good and was accepted until developments on these same two areas during succeeding years again confused the issue of percentage control. For the seasons of 1914, 1915, and 1916, the infestation in the Craggy Mountain unit continued in the endemic condition found in the spring of 1914; then a sudden increase of 249 percent in 1915, followed by a decline of 53 percent in 1916. It was found that the 1915 increase on the Barkhouse unit corresponded with a general epidemic condition which developed that same year in most of the watersheds of the Klamath and Rogue River areas. For some reason this epidemic outbreak by-passed the Craggy Mountain unit. These developments raised the question whether recleaning of the Craggy Mountain unit had been a factor in holding the infestation in that area under control, while the Barkhouse unit, which had been treated only once, was subject to the same epidemic condition that prevailed in untreated areas in 1915 and 1916. Assuming that the recleaning was effective in keeping the infestation under control, still another question suggested by these developments was how often and how intensively is it necessary to rework a control area in order to maintain satisfactory control and prevent epidemics.

As experience accumulated from other western pine beetle control projects following those initiated on the Klamath in 1912, the controversy over percentage control was largely obscured by the practical considerations involved in its application. It was gradually realized that the core of the problem was not what percent of the infestation should be treated but how much of it could be treated under varying area conditions, types of infestation, timing of control work, and different methods of eradication. If its application required continued working of the same area year after year, then techniques adapted to maintenance control were needed, and these had not been attempted in any of the earlier control projects.

Following the Klamath projects, both Forest Service and Bureau of Entomology workers concerned with bark beetle control became interested in plans for an experimental program to test methods and strategy for maintaining control over long periods of time. Plans for this experimental work were developed through a series of conferences at Ashland, Oregon, from 1917 to 1920 and were reported upon by Miller, Hopping, and Jaenicke (U177). These plans culminated in recommendations for the San Joaquin project which was a five-year program of experimental work to test the possibilities of maintenance control.

Maintenance Control - the San Joaquin Project

The ideas underlying maintenance control are too obvious to require elaboration. If a small amount of control work carried out at just the right time can prevent an infestation from developing into a serious epidemic outbreak, then timely action is far preferable to waiting. The advantages of preventing waste to timber and high costs of control which are inevitable after the epidemic has developed are so great that maintenance control should justify the use of relatively expensive methods.

In his discussion of "How to Maintain Control," Hopkins (43) suggested that this work could be taken care of by rangers and fire wardens. He did not go into detail of procedure further than to specify that "it is not necessary that every infested tree should be treated, but it is of special importance that all groups of infested trees should receive prompt attention." Such considerations as status of infestation under which control should be undertaken, size of area which should be covered, timing of control, results to be expected, and other practical problems to be encountered in the application of maintenance control were not touched upon by Hopkins. The San Joaquin project was the first attempt to find the answers to a number of questions that become important in considering the application of control under endemic rather than epidemic infestations.

Through the five years that it was in effect, the San Joaquin experiment explored a number of phases to determine (1) what methods are best adapted to maintenance control, (2) whether it is possible to reduce endemic losses below those that occur in nature, (3) whether epidemic increases can be prevented before they develop, and (4) whether the amount and value of the timber which can be saved will offset the cost of maintenance control.

Following a number of preliminary and progress reports, the project was summarized by Miller (U186) soon after it was closed down in the fall of 1924. This final report entitled, "Control of the Western Pine Beetle on the San Joaquin Project," analyzed the results that were obtained from a diversified and detailed series of experiments. A more condensed summary by Miller (85) is quoted below:

> "An area of some 80,000 acres of ponderosa pine type on the Sierra National Forest which had previously been under observations for some years was selected as the testing ground for the maintenance control idea. For this type of forest, the condition was regarded as endemic if the number of infested trees per section ranged from 25 to 50. Direct control work had been carried on during the period from 1913 to 1917 in parts of the area where losses of this severity had existed. The experiment was planned with the idea of trying out various methods and systems of control application, the course of the infestation was followed not only on the control areas but also on check areas which represented as closely as possible similar infestation types and conditions.
>
> "In the five successive seasons during which the project was in progress, the work was carried through three fairly distant phases.

"1. A general working over of the entire area with cut-peel-burn control to make sure that the infestation was everywhere reduced to an endemic annual loss of 25 trees per section or less. This phase was completed in the spring of 1920.

"2. Follow-up work which consisted of a patrol of the entire area with small mobile crews of 2 or 3 men who treated accessible infested trees whenever they could be found during the spring, summer, and fall periods. This work was planned so that the cost would not exceed 5 cents per acre. The objective was to detect increases as they were starting and to destroy enough of the broods to ward off incipient epidemics.

"This system of work was carried on during 1920 and 1921, using cut-peel-burn in the spring and late fall and solar heat during the summer. Less than 40 percent of the seasonal infestation was found and treated, but this was not sufficient to maintain control of the western pine beetle. On the control area that was worked, the infestation increased and decreased to the same extent as it did on the check areas where no control work at all was done.

"3. Because the light intensity of area coverage followed under (2) did not give satisfactory control, the project was given over during its final three years to an attempt to determine whether treatment of a high percent of the infestation would yield better results than those obtained by treating only 40 percent or less. This phase of the study was carried out by working small unit areas of from 3200 to 6000 acres using a different method of area coverage on each unit. The intensity of treatment varied from treating only the overwintering infestation to attempted extermination. None of the four units selected for control work had complete isolation from adjoining timbered units.

"On the areas that were worked less intensively, it was found that control work accomplished the treatment of from 40 to 50 percent of the total seasonal infestation. When compared with check areas, no appreciable effect of control was found since the infestation increased and decreased to about the same extent as it did on nearby areas where no control work was done.

> "On the extermination unit, which was spotted every three weeks throughout the season of beetle activity and infested trees treated as soon as found, it was possible to treat about 90 percent of the total seasonal infestation. Under this degree of intensive work a reduction of 19 percent in the volume of infestation was secured while a 67 percent increase occurred in the check area. However, under the current stumpage price of $3. per M, the value of the timber that was saved did not equal the cost of this intensive maintenance work. Computations indicated that if the timber had been worth $6.70 per M, the cost of maintenance control would have been covered by the value of the timber that was saved."

The general conclusions to be drawn from the San Joaquin maintenance study can be summarized as follows:

(1) Continued maintenance control, regardless of the percentage of infestation treated, increases in relative costs, and decreases in comparative effectiveness during a decreasing endemic infestation.

(2) Only very intensive maintenance work is capable of preventing an increase of infestation when the natural tendency is upward.

(3) The treatment of 100 percent of the infestation on a small area each year does not "exterminate" the beetles and is impracticable.

(4) In commercial pine areas, maintenance control by direct methods against endemic infestations is not warranted economically unless the treated trees can be utilized. Sanitation-salvage is far more effective and practical as a method of maintenance control.

(5) In special areas where there are high esthetic values or other considerations which fix a high value upon existing tree cover, maintenance control by direct methods can be justified.

Policy Applying to Direct Control

There are many economic as well as entomological considerations that must be taken into account in making decisions as to when and where direct control of the western pine beetle is justified. For this reason, general policies to govern control recommendations are not easily defined. Nearly every control project that has been undertaken has had its own special conditions affecting control policy. Such general rules as have been prescribed must necessarily touch only on the more salient factors.

Craighead, Miller, Evenden, and Keen (26) summarized the results of western pine beetle control that were evident up to that time and on this basis drew up a policy statement:

> "1. The success of direct western pine beetle control has not been spectacular or outstanding but in many cases has shown tangible results.
>
> "2. One season of thorough work results in reduction of losses.
>
> "3. The benefits are greatest when the natural trend of infestation is upward.
>
> "4. The benefits are temporary and must be continued to maintain control. Under these conditions we recommend direct control after considering both economic and entomological factors.
>
> "In parks and on recreational areas where trees are of high value from the esthetic standpoint.
>
> "On small well isolated areas where the timber is of high value and where the entire infestation can be treated in one season.

> "On large areas, preferably with partial isolation, where the entire infested area can be treated and where it is to be logged within 3 or 4 years.
>
> "In commercial stands, whether isolated or not, where control work can be supplemented by logging and the treated trees salvaged at a low cost or a profit. Such work may be combined with selective logging to remove susceptible trees and produce better growth conditions in order to give permanent protection for long periods."

In 1935 the Branch of Forestry of the National Park Service (127) set up the insect control policy to be followed on national park areas. After defining the types of areas in which insect control would be considered, the forestry branch made the following statement specifically for the western pine beetle:

> "This beetle takes annually a small percentage of the stand and at intervals of some years a considerably larger percentage. The main objective in controlling the depredations of this beetle would be to prevent the peaks of this type of infestation and thus prolong the life of the existing stand over a longer rotation of gradual replacement; in other words, the objective would be to carry on a certain amount of maintenance control from year to year in an effort to keep the losses at the lowest possible status all the time."

With the outstanding success of sanitation-salvage in controlling western pine beetle epidemics, particularly in commercial stands, the policy in respect to using direct methods was greatly modified. Sanitation-salvage was recommended in all interior ponderosa pine type where the timber could be cut and utilized. Direct control was then limited to a restricted number of situations which were outlined by Keen (U162) in a new control policy statement on April 1, 1949.

"Direct methods of bark beetle control may be recommended in situations where sanitation-salvage is not applicable and where the following conditions apply:

"A. Entomological conditions.

"Strong broods of bark beetles in single trees or small groups and infestation showing signs of increasing aggressiveness and an upward trend. Endemic infestation will not be treated except as maintenance control in highly valuable recreational areas or where cost can be largely offset by salvage. Epidemic infestations may be treated to hasten decline but if advanced too far, may be considered as beyond practical control measures. The entomological considerations warranting control cannot be stated precisely but require the exercise of good judgment based upon technical factors and past experience.

"B. Area conditions.

" (1) Park or recreational areas with or without complete isolation where trees are of high value from an esthetic standpoint. Annual maintenance control is justified in such areas.

" (2) Small areas, well isolated from other infested areas, so entire area can be treated in one season. Recleaning in the second season depends upon character and intensity of new infestation.

" (3) Large areas, preferably with partial isolation, where the entire infested area can be treated, and which are to be logged or come under management within three or four years (before reinfestation develops). Recleaning in the second season depends upon character and intensity of new infestation.

" (4) Commercial stands, whether isolated or not, where control work can be supplemented by logging and the infested timber can be salvaged at a low cost or a small profit. Wherever possible, such work should be combined with selective logging to remove susceptible trees and produce better growth conditions in order to give protection for longer periods of time.

"C. Economic conditions.

"While the entomologist must take cognizance of economic considerations, the economic justification for control is a matter which must be decided primarily by the timber owner. In general, the cost of control work should not exceed the value of benefits to be derived. The benefits include: (a) actual timber values saved; and (b) intangible values - such as protection of watershed cover and grazing, esthetic values, and reduction of fire hazard. In parks and highly valuable recreational areas, cost may be high and still be justified by the esthetic values involved. On commercial areas the cost of control if applied against an increasing infestation might be justified up to three to five times the stumpage value of the timber infested, while with decreasing infestations, the treating cost per thousand board feet probably should not exceed one-half the value of the stumpage.

"On the basis of present knowledge and the general considerations discussed above, the Bureau's policy in regard to control of the more important western pine bark beetle species in the Pacific Coast states may be briefly summarized as follows:

"Direct control of western pine beetle populations.

"If infestations show signs of increasing due to lack of, or in spite of, preventive measures, then direct control is warranted under the following conditions:

"(1) Park and recreational areas of high value. Requirements: Strong, aggressive broods found in single trees or small groups, any intensity. Treatment: Annual maintenance control is justified.

"(2) Commercial timber areas - west slope Sierra Nevada and Cascade Mountains, north coast, and southern California.

"Infestation in this subregion, while normally of low endemic character, tends to build up rapidly to epidemic proportions. These are often preceded by an epidemic of top-killing attacks on mature trees or group attacks of immature ponderosa pine by Ips confusus, or may develop as a result of windfalls, fires, logging, slashings, or drought conditions, all of which are conducive to the rapid breeding of strong beetle broods.

"Requirements for control: Definitely increasing, aggressive infestation in group formation. Area and economic requirements as stated under B and C above.

"Treatment: One season of direct control hitting all group infestation in control area, followed by a second season of control if group attacks persist. Maintenance control of endemic infestations or control of declining infestations not justified, except where cost can be offset by salvage.

"(3) Commercial timber areas - east slope of Sierra Nevada and Cascade Mountains.

"Infestations of recent times characteristically persistent and normally of high endemic status; periodic epidemics of great intensity killing from one to 15 percent of the stand in a single year.

"Requirements for control: Increasing, aggressive infestations or epidemic infestations which cannot be handled by sanitation-salvage logging may be treated by direct control methods. Declining epidemics may be treated to speed decline. General considerations as to area and economic conditions, under B and C above apply.

"Treatment: Direct control should be thoroughly applied to the entire infested areas; 100 percent spotting is needed. This may be followed with a second season of recleaning if group infestation persists. Maintenance control, except on a salvage basis, is not justified because of small effect on endemic infestations and high annual cost. Sanitation-salvage is much more effective in beetle control than direct control measures, and should be used wherever possible."

BIOLOGICAL CONTROL

Ever since the inception of bark-beetle control, those concerned with the work have been looking for an easy way to control the western pine beetle. All the direct control methods which have been developed thus far have required much labor and the costs have been considered high in proportion to the benefits derived. Timber owners and foresters regard these methods as the hard way to control beetles and it was only natural that they should expect entomologists to find some way to exploit the natural factors that control the beetles for the benefit of the timber owner.

Perhaps the first ideas along this line were suggested by the work of woodpeckers which feed upon bark beetle broods in infested trees. This activity of the birds was a matter of common observation on the early control projects. Men on the treating crews, whose duties required the tedious peeling of infested bark, were prone to advocate the establishment of a "woodpecker farm" to raise birds for liberation in infested areas. This idea, however, never achieved serious consideration. Studies that were made by Keen, Patterson, Person and Rust (Section III, pages 206-209) on the feeding habits of woodpeckers indicated that, while these birds were undoubtedly beneficial, they were not as effective as predators as they appeared to be. Even at best they devoured only a limited percentage of the bark beetle broods and even seemed to show a preference for the beneficial clerids. Hopkins (43) pointed out that birds could have little effect upon a bark beetle epidemic because they could not increase their numbers nearly as fast in proportion as the beetles could multiply.

Another idea that has been given consideration is the use of insect parasites and predators to establish control. A number of these have been listed and their habits and control effects in nature are discussed in Section III, pages 210 -223 . Parasites of the western pine beetle were soon dismissed because of their relative scarcity in nature and the physical conditions which limit their effectiveness. However, the native insect predators of the western pine beetle seemed to offer some possibilities for biological control, and a considerable amount of study and experimentation has been done to explore possibilities for the use of these insects. Some of these studies have led to modification of direct control practices in order to protect the predators, although no satisfactory method of biological control alone has yet been found. At least three methods have been proposed for protecting and increasing the insect predator population within an area.

Protecting Insect Predators under the Cut-Peel-Burn Method

The first studies in 1923 on the biology of the clerid predators by Person (U224,U226) brought to light the fact that a considerable percentage of the larvae migrate down the tree as they mature and pupate in the bark around the base of the stump and in the surrounding duff. Under the cut-peel-burn method it had been customary to peel the stump and burn all bark around it, a practice which was obviously destroying the beneficial clerids. After the discovery of this pupation habit, the cut-peel-burn method was modified so as to avoid burning of bark around the stump. This was first stated in the control manual issued in 1927 by Keen (60):

> "The fire line should completely encircle the tree (after falling), but exclude the stump. This precaution is advisable since many predacious insects pupate in the soil at the base of the trees containing advanced broods of beetles, and by preventing the burning of debris around the stumps these insects are saved."

There is no record of any studies to determine the actual control effect upon western pine beetle populations when this precaution is taken, but it is obviously good practice and is generally followed wherever conditions permit on control projects.

Protecting Clerids where the Solar Heat Method Is Used

Person (106) proposed a method for increasing the effectiveness of the clerid, Enoclerus lecontei Wolc., in its predation upon western pine beetle broods in areas where the solar heat method of control can be used. His studies had shown that when unpeeled infested logs were exposed to the hot sun, the clerid larvae migrated from the top to the shaded underside of the log and survived; but the bark beetle broods, being unable to move, were killed on the top but survived on the lower sides and bottom. Then if the log were turned over, the clerids would again migrate to the underside, but the bark beetle broods which were turned up to the sun were killed when the log was rolled. Person figured that if infested logs were exposed during hot weather and rolled three times so that each third of the circumference received direct exposure to the sun, that most of the pine beetle broods would be killed and most of the clerids would survive. In this way, the ratio of predators to beetles could be increased and the effects of predation multiplied. This proposed method has never been tried in actual control, mainly because the conditions under which solar heat control can be used effectively are so limited that it is rarely used on direct control projects.

Artificial Propagation of Predators for Liberation in Infested Areas

Interest in this method of biological control for bark beetles was no doubt stimulated by its widely publicized success on a few agricultural pests. Forest entomologists have been none too optimistic over the feasibility of using this method in the forest. The only predators available were the native species and their populations are being maintained at as high a level as can be expected under natural conditions. The only apparent method of increasing these predators in a local area is to rear them under insectary control and then liberate quantities of the adults. That Nature's method of producing these insects could be improved upon by artificial techniques seems questionable.

The forest insect laboratory at Berkeley decided to give artificial propagation of predators a trial, first of all to settle the question of whether it was practical and also work out obscure points in the habits and food requirements of the predators. The project was undertaken with two of the most important predators of the mountain pine beetle, *Enoclerus sphegeus* F. and *Temnochila virescens* F. The clerid, *E. sphegeus*, is limited in its host selection and is found most commonly with the mountain pine beetle; but the trogositid, *T. virescens*, has a long list of insect hosts and is a very common predator of the western pine beetle. The experimental work was carried on at the Miami field laboratory by Struble during the seasons of 1938-41.

Struble began [by starting] with the eggs of the predators and tried various methods of incubation and of feeding the larval stage through to pupae and adults, under laboratory conditions. He used a number of food media, mostly insect larvae. The trogositid responded best to substitute hosts, but it was found that the best development was obtained when bark beetle larvae were used. The greatest difficulty in rearing developed because of the cannibalistic habits of the predators. They devoured each other when narrowly confined, making it necessary to rear them separately. [if kept within limited confinement and it was necessary that each larva be reared in a separate cell.] Normal, healthy adults were produced when predator larvae were kept in separate glass vials and fed frequently on larvae of the mountain pine beetle. A stock of mountain pine beetle broods for feeding the predators was maintained at the laboratory by infesting ponderosa pine logs in a screened insectary. This successful technique of rearing required a considerable amount of labor and material for the number of adults produced.

The results of these propagation experiments were published by Struble (120) in 1942. He figured that the labor and material costs would average around $125.00 for each 1,000 adults produced and concluded:

> "Although mass production and greater improvements in methods of rearing through use of substitute hosts may greatly reduce this figure, it may still be too high to be practical. The main reason for this is the necessity of handling each predator larva separately... The cost of rearing these predators by use of their native hosts as food is much too high for practical purposes. Furthermore, the set up of logs in which to rear the host is too cumbersome and is wasteful of green timber... Unless methods can be developed which will overcome these objections, there is little hope of increasing the beneficial effects of these predators beyond that of protecting them in nature."

PREVENTIVE MEASURES

The possibilities of protecting individual trees from bark beetle attack had not been overlooked. The development of a protective spray or other means of saving individual trees would be of great service where pines are of special value as shade or ornamental trees, particularly in parks and recreational areas. Many protective measures have been tried but so far, none have been completely successful.

Screening

Screening the trunks of individual trees with wire mesh so that the beetles could not get at them was one of the first measures tried in preventing bark beetle attack. This has not been attempted with the western pine beetle, but according to Gibson (U68) it met with some success in preventing attack on lodgepole pines by the mountain pine beetle. Patterson (U215) also had success with screens in preventing attack on lodgepole pines at Crater Lake National Park in 1926. The method, however, seems to be impractical with the western pine beetle because it would require a finer mesh screen and because it would be quite difficult to install the screen in the mid-bole and top of large ponderosa pine trees where the beetle usually starts its attack. In the case of lodgepole pine, it was necessary only to screen the lower 25 feet of the bole to prevent attack.

Tanglefoot

The possibility of using a sticky substance which would trap the adult beetles on the outer bark was tried in 1937. The California Chemical Spray Company offered a liquid tanglefoot under the trade name of "Dead Line" which could be sprayed upon the bark. This was tried on logs under cage control at the Berkeley Laboratory and reported upon by Struble (U292). The hard-shelled beetles were able to plow through the sticky "Dead Line" and enter the logs without much difficulty. A very few dead beetles were found stuck upon the surface. Obviously, this material was designed to hold soft-bodied insects, but the strong crawling habits of Dendroctonus beetles, which enable them to work through the sticky pitch tubes, make it extremely doubtful if any tanglefoot compound can be developed which will hold them.

Repellents

The use of repellents or toxic chemicals to prevent bark beetle attack has been tested for a number of substances. In 1931, Struble (U286) tried out several patented insecticides which had been proposed by commercial firms as a sure cure for the pine beetle problem. Struble tested these against the fir engraver beetle on white fir as that was the project he was then concerned with. The material included flusi-dust (sodium fluosilicate), creosote emulsion, Bolite, paradichlorobenzene in linseed oil, and Thymol. The results of these experiments led to the conclusion that: "The use of these chemicals by applying them externally does not seem justifiable because (1) the toxic or repellent effects do not last long enough and (2) the mechanical composition of fir bark does not permit penetration to any appreciable depth." The same objections seem to apply equally well to the use of these materials as repellents of the western pine beetle.

Experiments to find a specific repellent for the western pine beetle were taken up by Norman Gay of the Standard Oil Research Laboratory in 1932 and were recorded in field notes by Struble. Gay's tests were made by exposing green trap logs in the field and also in cages with numbers of adult beetles. The materials tried were sprays consisting of (1) an asphalt emulsion which solidified on the bark surface forming a hard coating nearly one-fourth inch thick, (2) an oil-naphthalene mixture (24061R) and (3) an oil-paris green mixture. In all tests the beetles succeeded in boring through the materials on the outer bark and establishing attacks in the green phloem. If there was any repellent effect from the sprays, it was obviously overbalanced by the attraction of the green logs. Some beetles apparently were killed in making their attacks, but the fact that enough adults did get through to completely infest the logs disqualified all of these materials as repellents or control agents.

Residual Sprays

With the availability after World War II of the newer, more potent insecticides such as DDT and BHC, which leave residual deposits of lethal intensity, the possibility of developing protective sprays was greatly increased.

Patterson (U222) found that Ips could be prevented from attacking piled fresh slash when this was sprayed with a 5% DDT solution in diesel oil. Attempts to prevent attack by spraying standing trees were inconclusive because none of the trees, either treated or untreated, were attacked.

More recent experiments by Perry (U223) and Moore (U204) of the Berkeley Laboratory indicate that control of D. brevicomis with residual-type sprays may well be possible through systematic development of formulations and application techniques.

INDIRECT CONTROL THROUGH FOREST MANAGEMENT PRACTICES

From the studies of ecological relationships (Section IV) came the realization that the western pine beetle was practicing a primitive form of silviculture in ponderosa pine stands. Stands containing a high percent of mature slow-growing trees were more susceptible to infestations than stands made up of vigorously growing trees. The western pine beetle was making periodic thinnings which released trees from stagnation, removed the old susceptible veterans, suppressed, intermediate, and codominant crown classes, made openings for regeneration, and thus stimulated the growth of young trees. The result was an uneven-aged forest composed of even-aged groups. Moreover the beetles were determining the natural rotation of ponderosa pine on different sites (71, 73). With these clues, foresters have been developing a silvicultural system for ponderosa pine management which takes into account its natural habits and the part which the western pine beetle plays in its ecology.

The obvious approach to effective beetle control was through the use of silvicultural measures, which conformed to the natural ecological pattern, and which would maintain a healthy, resistant condition in the growing stock of trees in the reserve stands. Methods that have been considered include surface burning, stand improvement thinnings, selective logging, and a modified form of selective logging known as sanitation-salvage. None of these methods involved the killing of broods of beetles and are, therefore, quite indirect in their control effects.

Surface Burning

That the amount of ground cover consisting of brush and dense stands of reproduction is related to bark beetle hazard was brought out by Bedard (U18) in a study analyzing certain hazard factors in eastside pine stands. Weaver (132) also came to the conclusion that the heavy understory of pine poles and reproduction in pine stands growing under limited moisture conditions resulted in such severe competition with the mature trees that heavy depletion by bark beetles was inevitable unless the understory was kept down. Periodic light fires offer one way to keep the understory suppressed to the point where it will not deprive older trees of available soil moisture. This is the basis for the argument that periodic controlled light burning will keep the merchantable stand in a resistant condition and thus act as an indirect control measure against the western pine beetle.

That light or surface fires have been beneficial in reducing bark beetle damage, after the first few years of increased losses due to fire injury, has been shown on a number of areas studied (See Section IV ,pages 471-475). Although studies and observations have indicated that burning may be beneficial in reducing bark beetle damage, many disadvantages connected with the use of fire must be taken into account. Considerable injury to growing stock may result from light burning, which will increase bark beetle damage for a period of years. The enlargement of fire scars on mature trees will increase breakage and windthrow. This will often set stand volumes back to such an extent that it will take many years of improved growth and lowered bark beetle damage to recoup these losses. The hazards involved in the use of fire for cleaning out the understory and its objectionable silvicultural effects will probably continue to preclude its adoption as a control method.

Stand Improvement Thinnings

Stand improvement projects that have been undertaken to date in the pine region were designed primarily as silvicultural experiments and insect control considerations were entirely secondary. In 1934 a number of thinning projects were carried out in the California region on which forest insect developments resulting from the operations were followed by the Berkeley forest insect laboratory. The chief entomological concern on these projects seems to have been the possibility that Ips and other bark beetles would develop in the slash and produce attacks in the green stand left after the thinning. Salman (U264) in summarizing the results of the thinning projects concluded that:

> "There does not appear to be any great hazard (of western pine beetle build up) created by cutting of small sized reproduction and poles. A hazard does appear to be created by cutting large sized material, particularly if it is felled in a group of trees of similar or larger dimensions."

On the whole, the results of these preliminary improvement thinnings appear to have little application to western pine beetle control because the stands selected for treatment have been made up largely of young trees which had not reached the diameters and ages that favor infestations.

Selective Logging

The main idea behind control of beetles by selective logging is based on the premise that some trees are much more attractive or susceptible to beetles than others, so that if these trees are removed then the residual stand will be made up of the more resistant trees. The beetles will then find conditions unfavorable for maintaining their populations and they will not be able to produce epidemics and serious losses. The entomological considerations to be taken into account in the application of this method of control center around the following questions: (1) Which are the susceptible trees? (2) How can susceptible trees be distinguished from resistant trees? (3) To obtain control, is it necessary to remove all trees showing indications of susceptibility, or will removal of only the most highly susceptible trees suffice?

The basic factors underlying these questions have been discussed under ecological relations of the western pine beetle in Section IV, pages 334-394, and their application to selective logging practices will now be considered.

Removal of the Slower Growing Trees

The first attempt to use selective logging as a control measure was based on the selection of trees to be cut almost entirely on the basis of growth rate. Person's earlier work pointed to suppressed growth rate as the dominant factor in the selection of trees by the western pine beetle, and to the possibility of using growth rate as an index in marking trees for logging operations designed to reduce the beetle hazard. In 1929 a preliminary experiment was undertaken to put this theory to a test (U233). One of the 40-acre plots (Timber Mountain) on which tree susceptibility had been studied was selected for this test; on 20 acres the trees considered to be susceptible were selectively logged and the remaining 20 acres were left untreated as a check. The experiment was described in two reports by Person (U234,U238). The trees were selected for cutting on the basis of a growth rate of less than 1 mm. per year and the silvicultural requirements necessary to leave an adequate reserve. On the treated plot, 53 percent of the susceptible trees were logged, amounting to 59 percent of the stand volume. Because of the extremely low average growth rate of trees on this plot, it was not possible to remove all trees considered to be susceptible and still leave an appreciable reserve so only the most susceptible trees were removed.

Progress reports on the Timber Mountain selective logging experiment were prepared by Salman (U251) and Salman and Bacon (U254). The final results were summarized by Salman (U258), who concluded that the control results were inconclusive due to the unfavorable conditions under which the test was conducted. The site was marginal and the entire area surrounding the 20-acre plot was subjected to severe epidemic infestations for the 5-year period following logging. Salman stated:

> "Under the environmental conditions affecting the stand included in this experiment, the cutting and removal of unthrifty and susceptible trees to the extent of 59.5 percent of the volume had not resulted in any marked reduction in the intensity of the infestation or saving of timber other than that utilized in the cutting operation."

Removal of Susceptible Tree Classes

Indirect control through selective logging was measurably advanced by the development of tree classifications based on age and crown vigor (See Section IV, pages 379-382). Keen (67) stated: "Once the type of tree most likely to be killed (by pine beetles) can be recognized with a fair degree of certainty, it is possible to make partial cuttings of beetle-susceptible trees, either for the purpose of salvaging valuable high-risk trees before they are damaged by beetle attack or for the silvicultural objective of reducing mortality and increasing net growth." Keen showed that 8 of his 16 tree classes, particularly those of C and D crowns, were of highest beetle risk, and suggested two types of cutting (1) a salvage cut of 14.4 percent of volume limited to the 4C and 3C trees of highest risk and value, and (2) a preventive treatment taking all of the susceptible types and removing approximately 56.4 percent of the volume.

Keen's classification was first put into use in 1935 in the "Hines Study" on the Edward Hines Lumber Company's logging operation on the Silvies Working Circle of the Malheur National Forest in Oregon, where the "maturity selection system" was being developed by Brandstrom (8), and in 1936 was applied to a "thrift selection" cut on this same working circle. In each case a 40 percent cut of the stand volume was involved. Earlier cutting on this area had been on the basis of standard Forest Service practice of marking approximately 80 percent of the volume.

This area provided the site for a study by the Forest Insect Laboratory at Portland to determine the effect of these different cutting practices on timber mortality from bark beetles. The study was initiated in 1937 by the establishment of a series of six 320-acre plots in each of the three types of cutting. Whiteside (U326) summarized the loss records for the period 1937-1944, and presented results of the study for the eight-year period.

The three methods of cutting used on this logging operation were defined by Whiteside (U323) as follows:

1. Standard Forest Service 80% selection. Cuts of approximately 75 to 80 percent of the pine volume in the older and least thrifty trees. Rules not rigidly defined as to tree classes, but the younger classes and at least one seed tree per acre left. All snags felled and slash burned. The cutting made in this area during the period 1930-1935, inclusive.

2. Forty percent economic or "value selection." Trees for cutting were selected on the basis of the maturity selection rule of earnings. After considering growth rate, mortality rate, and earning rate, only trees which would net the operator at least $2.50 per Mbm were marked. While value determined the selection, in some cases trees in classes 3A and 3B were left as substitutes for lower valued trees in classes 4C and 4D over 22 inches D.b.h. However, these substitutions were limited to not over 10 percent of the cut. This area was cut during the period 1935-1938, inclusive.

3. Forty percent silvicultural or "thrift" selection. The marking rules were applicable to trees in classes 3 and 4 provided that no trees under 22 inches d.b.h. were to be marked. All class 4 trees above this limit were to be cut unless needed for seed trees or to fill openings. No class 3A trees were to be marked and trees in classes 3B and 3C were usually left unless they were undesirable as part of the reserve stand. In this area the cutting was done during the period 1936-1939, inclusive.

The study plots showed that following cutting there was an immediate reduction in insect loss for the first year. Then in the second and third years, undoubtedly due to the effect of logging disturbances, there was a marked increase in losses. After the third year, the trend of losses dropped sharply each year to the sixth year, at which time they could be classed as low endemic.

The average annual gross mortality, including beetle-kill and windthrow over the eight-year period following cutting (seven years on the thrift plots) is shown in the following table:

Plots	Average annual mortality			
	Board feet per acre		Gross % of stand	
	Insect	Total	Insect	Total
Virgin	69	85	0.43	0.54
40% value cutting	53	55	0.55	0.57
40% thrift cutting	33	37	0.29	0.33
80% F.S. standard cutting	16	17	0.35	0.36

It was found that the western pine beetle accounted for about 72 percent of the recorded mortality, while 16 percent was attributed to windthrow. In explanation of the above table Whiteside noted that many trees on both virgin and cutover plots received injuries which predisposed them to beetle attacks in 1943 and 1944. Of these, lightning-struck trees, subsequently killed by the western pine beetle, were the most numerous.

Growth studies were not available at the time of Whiteside's report to appraise the amount of release resulting from the different systems of cutting. However, it was found that the general growth trend was definitely upward after 1939 with the 1942 growth well above normal, on both cutover and virgin plots.

As would be expected, the above table shows that the heaviest cut resulted in the least subsequent board foot loss. However, in proportion to the residual stand, the least insect loss followed the "thrift" cutting in which all susceptible trees above 22 inches d.b.h. were removed. A somewhat higher loss, of 0.35 percent of stand volume, occurred on the 80 percent cut, while the 40% "value" cut showed a loss in excess of that on virgin plots. This was due to the high percentage of high-risk trees of low merchantability that were left in these stands.

After 1936, light selection cuttings primarily designed to remove the more susceptible tree classes, but also taking into account merchantability, became the rule on Forest Service and Indian Service timber sales in eastern Oregon and Washington, and on some private holdings such as the J. Neils Lumber Company's operation at Klickitat, Washington. The primary purpose of these cuttings was to get over areas of high beetle hazard [areas] as quickly as possible with a light cut to "beat the beetles" to the high risk trees and also to salvage those trees of high value which might be lost (80).

Keen's ponderosa pine tree classification has continued to be used as a silvicultural tool in timber marking in the interior ponderosa pine type of the Pacific Northwest and elsewhere, where removal of beetle susceptible trees is a primary consideration.

Sanitation-Salvage

For the purpose of beetle control a greater refinement in designation of high-risk trees was developed by Salman and Bongberg (114) for use in experimental trials at Black's Mountain Experimental Forest in California. From this work the term "sanitation-salvage" has come into general use to designate the removal of highly susceptible trees from the stand as a method of indirect bark beetle control.

Black's Mountain Experimental Forest, California, 1937-1944.— The Black's Mountain Experimental Forest served as the first pilot test of the sanitation-salvage method for control of the western pine beetle. This area, located in Lassen County, California, comprises nearly 10,000 acres of eastside ponderosa pine type with some Jeffrey pine. The area is managed by the California Forest and Range Experiment Station for the purpose of testing the practical value of theories of management, silviculture, and insedt control, which have been proposed for this forest type.

In 1933, when management plans were first formulated for the area, heavy infestations of the western pine beetle were present in the pine stands. These were treated by the direct cut-peel-burn method in 1934, and timber losses were reduced from an average of 202 board feet annually during the 1933-36 period to 73 board feet per acre in 1937.

"The application of sanitation-salvage cutting for the removal of high risk trees as a measure to reduce insect-caused loss was first employed on the experimental area in 1937," according to Bongberg (U26). "During that season 243 acres were cut. In the following three years an additional 1,320 acres have been treated by light selection cutting." A series of compartments were treated each year until 3,100 acres of the ponderosa pine type had been covered.

Under this sanitation-salvage program, all high-risk trees (Risk 4 and Risk 3) were removed. Where necessary, enough more defective or silviculturally undesirable trees were added to bring the total cut up to about 2,500 board feet per acre, or about 16 percent of the stand volume.

The first results of sanitation-salvage on this experimental forest yielded highly satisfactory control of western pine beetle infestations, according to Bongberg (U26), who reported that:

> "The comparison of loss conditions between treated and untreated areas has shown that as a result of cutting, losses were reduced the first year by 91 percent. Two years of loss subsequent to the cutting was 82 percent less on the treated area. For the three-year period, loss reduction has been estimated at 72 percent."

Figure 66 .-- Setting chokers on a 32-foot log on a salvage control project.

During the period following the start of this project, a series of progress reports were issued. One of these was prepared by P.C. Johnson (U121). Johnson discussed developments on the experimental area and explored methods of calculating beetle control benefits from sanitation-salvage in this area. The fact that the area was worked annually by small selected compartments and the treated area was extended from year to year during progress of the operation resulted in an annual change in the basis for comparison of treated and untreated areas. The procedure finally adopted consisted of four basic steps outlined by Bongberg (U35).

(Page 703a follows)

Figure 66.-- Setting chokers on a 32-foot log on a salvage control project.

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1. Tabulate annual measured loss on the untreated compartments and from this determine the yearly trend of the infestation under natural conditions.

2. Tabulate measured annual loss on treated compartments subsequent to cutting.

3. From the trend established on the untreated compartments (under 1), determine the predicted loss which would have occurred on the treated compartments if no control work had been done.

4. Compare the predicted annual loss with the actual measured loss on the treated compartments. The difference between predicted loss and measured loss following cutting represents the volume of pine timber that was saved, or in effect, the control benefits derived from sanitation-salvage treatment of the area.

The trend of infestation that was used for the comparison of treated and untreated areas is shown in Figure 67 . In this graph the measured loss on the untreated compartments for the year 1937 is used as the index, and the losses that occurred during the three preceding years and for the 10 years following are expressed in their ratio to this 1937 loss figure. The curve shows the trend of bark-beetle infestations for the total period, 1934-47, in those compartments where only natural control factors were operative.

Figure 67 .--Trend of bark beetle infestations in virgin stands, Black's Mountain Experimental Forest, California.

Using this curve as a base, it was possible to compare the actual measured mortality on the cut areas to the computed mortality which presumably would have occurred on these areas had they followed the normal trend. The results on an annual basis and for the 10-year period of record were as follows:

Reduction in beetle-caused pine mortality resulting from sanitation-salvage cuttings.

Annual basis		Cumulative basis for 10-year period	
1st year	86.1% reduction	1 year	86.1% reduction
2nd year	87.6 "	2 years	86.8 "
3rd year	91.8 "	3 years	87.8 "
4th year	87.7 "	4 years	88.2 "
5th year	87.0 "	5 years	87.8 "
6th year	83.9 "	6 years	88.1 "
7th year	86.2 "	7 years	88.3 "
8th year	76.9 "	8 years	88.8 "
9th year	74.8 "	9 years	86.9 "
10th year	66.7 "	10 years	70.7 "
Average	82.9% "		

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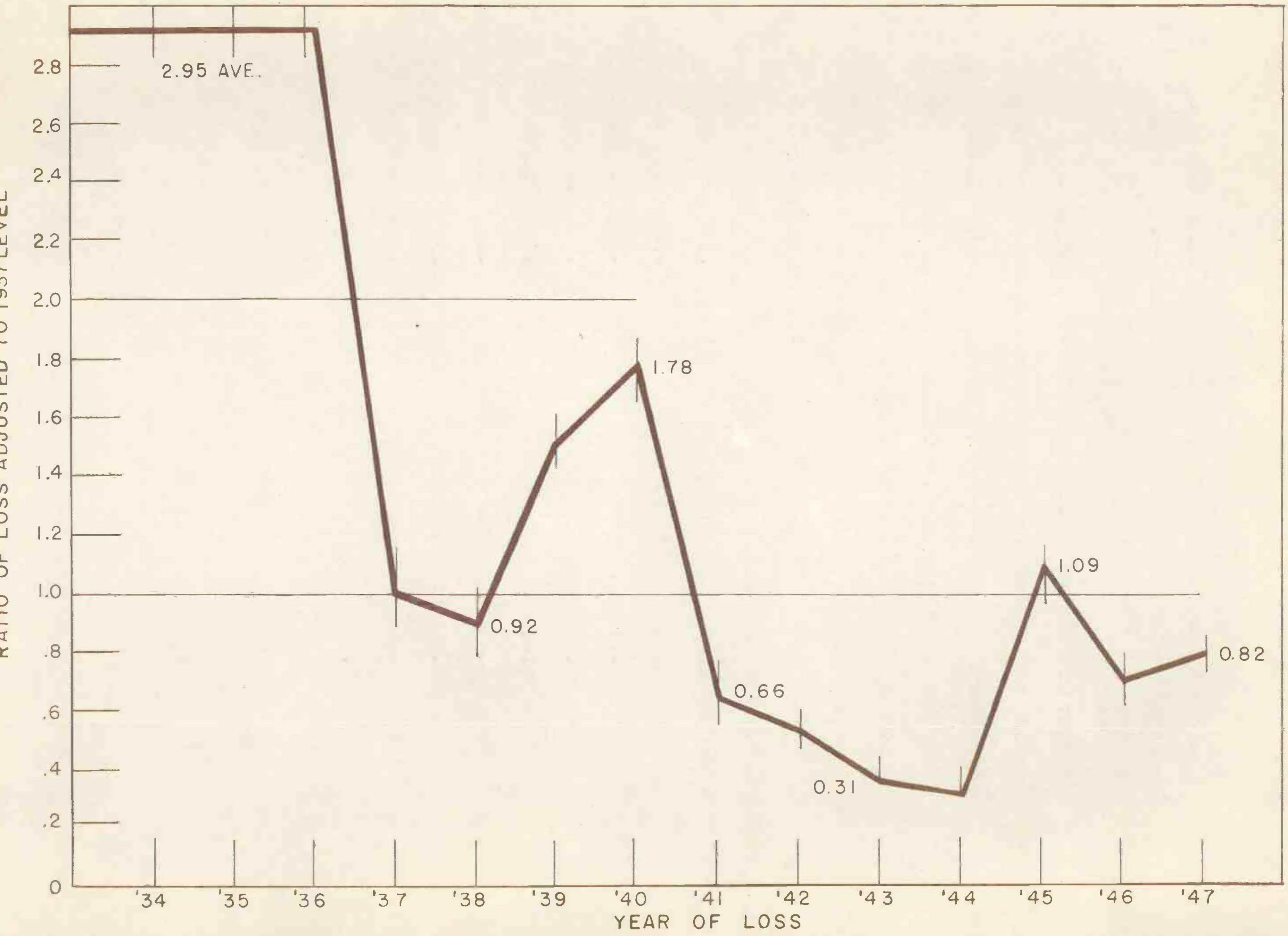
Figure 6[illegible]- Trend of bark beetle infestations in virgin stands, Blacks Mountain Experimenta[illegible]orest, Californi



Summary of Operation

1. Volume of Risk 4 and Risk 3 trees salvaged - 2680 B.F. per acre
2. Subsequent loss on treated area, 1937-1946 - 106 B.F. per acre
3. Expected loss if area had not been treated - 601 B.F. per acre
4. Volume of timber saved on treated area - 495 B.F. per acre
5. Average annual reduction ? in loss over 10-year period - 82.9%

The cumulative control benefits of the Black's Mountain project are shown graphically in Figure 68. This shows that a total of 495 board feet per acre was saved over a ten-year period from 1938 to 1947 inclusive.

Figure 68.-- Volume of pine timber saved over 10-year period following logging of high risk trees. Black's Mountain Experimental Forest, California, 1938-1947, inclusive.

Bongberg (U35) concludes:

> "Control results have far exceeded original expectations. Lasting benefits for periods up to 10 years are believed due to an upsetting of the normal ecological balance between the bark beetles and the host tree. Control results are conclusive evidence that sanitation-salvage logging is highly effective as a measure to be used for bark-beetle control in interior-type ponderosa and Jeffrey pine stands."

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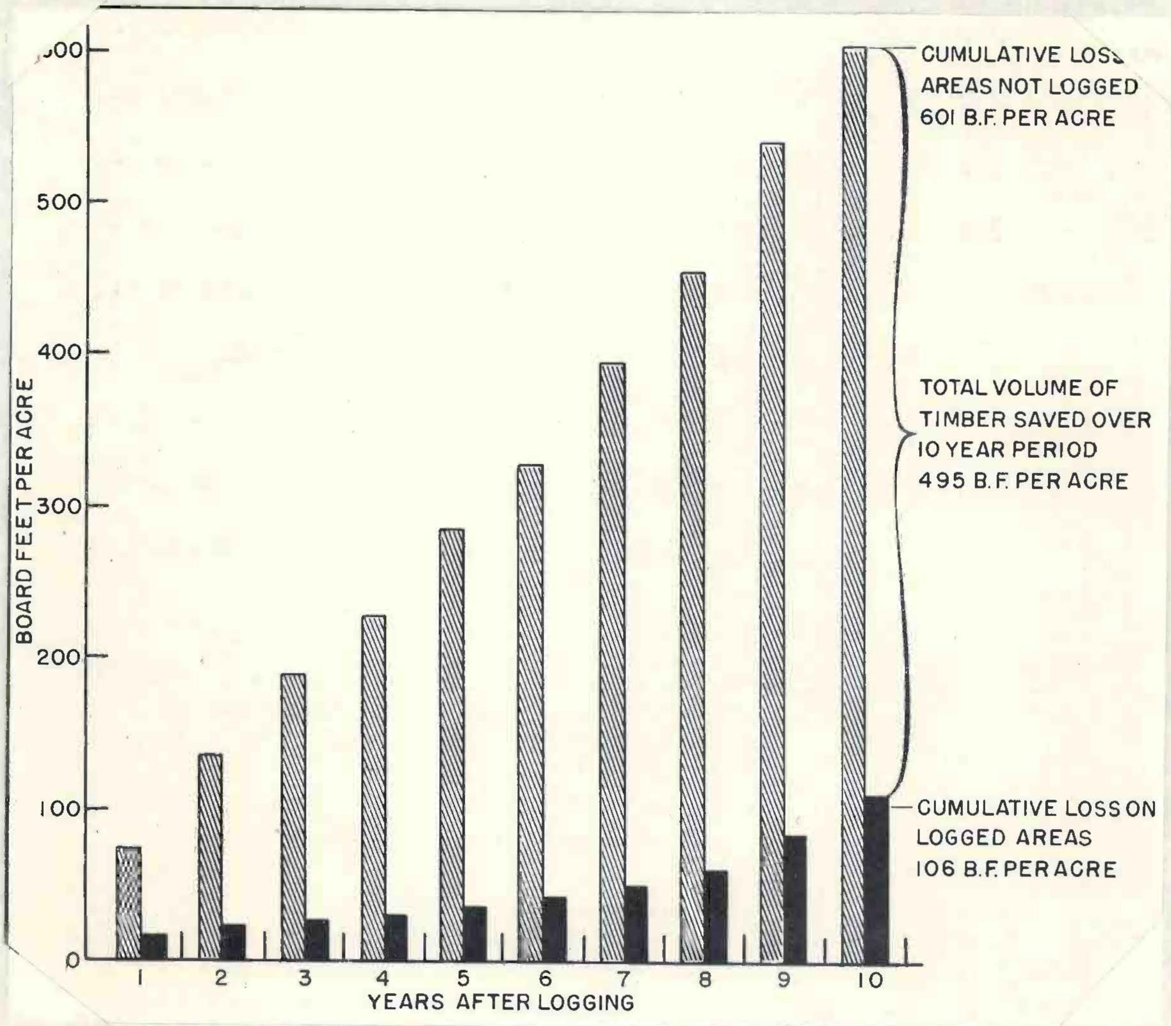

Figure 68.-Volume of pine timber saved over 10-year period following logging of high risk trees. Blacks Mountain Experimental Forest, California, 1938-1947, inclusive.

Dixie Valley Sale Area, Plumas National Forest, California, 1940.-- Following the demonstration of the methods of sanitation-salvage and their effectiveness on the Black's Mountain project, the Forest Service decided to test its practicability when applied where bark beetle control was needed on timber sale areas in the eastside pine type. The Dixie Valley sale area on the Plumas National Forest was first selected. This operation is described by Bongberg (U27). Because of sustained beetle losses, a tract of 8,000 acres was advertised for light selective logging in 1940, the Forest Service agreeing to mark not less than 25 percent of the green merchantable stand for cutting - about 75 percent of which was Jeffrey pine. While the risk characters which could be recognized in Jeffrey pine were similar to those in ponderosa pine, a new biological element was introduced in this project because of the prevalence of Jeffrey pine beetle infestation. According to Bongberg, "The chance to determine the effectiveness of this light treatment on areas of practically pure Jeffrey pine was important, since there were some indications that the Jeffrey pine beetle showed preferences in host selection unlike that of the western pine beetle in ponderosa pine."

It was estimated that about 15 percent of the green stand was made up of high risk, susceptible trees. In order to provide the minimum cut of 25 percent guaranteed to the logging company, it was necessary to supplement the entomological cut with other trees. This supplementary cut was made up of trees that were considered to be undesirable from a silvicultural standpoint. The entire Dixie Valley area was selectively logged in 1941 with a cut of about 3,500 board feet per acre or from 26 to 31 percent of the stand. The ponderosa pine losses were reduced by nearly 100 percent; but in Jeffrey pine, the reduction was about 82 percent the first year after cutting. The costs of logging were around 25 percent higher than for a regular operation, due to the amount of road construction that was necessary to open up the area and the relatively light yield per acre. This cost factor was an unsatisfactory condition for the logging company, which did not own the timber and, therefore, received no benefits from protection of the remaining stand.

In 1942 the Forest Service opened up further sanitation-salvage sales on the Modoc and Lassen National Forests, and rapidly extended the principle of sanitation salvage to most of their timber sales, both in eastside and westside types. (U29).

Cayton Valley Experimental Sanitation-Salvage Cutting - McCloud River Lumber Company - 1939.— Some private timber owners were not long in recognizing that sanitation-salvage is preferable to direct control, mainly because this indirect method can pay its way through the utilization of timber which would otherwise be lost, besides being more effective in reducing losses.

The first private sanitation-salvage control operation was started by the McCloud River Lumber Company in 1939 on a tract of 1440 acres of high quality eastside ponderosa pine type located in Cayton Valley, Shasta County, California. Another test on 600 acres was made on the Harris Mountain tract in 1940. Their purpose was to obtain protection from beetle losses over a five-year period, after which they expected to include the area in their regular logging program. They were also interested in determining the costs of this indirect method of control as compared with direct methods which they had been using previously over a period of many years.

Figure 69.— Mobile log loader especially designed and used by Bill Hanan for salvage logging. Old Station, California, 1952.

Special mobile loading and trucking equipment was purchased for the operation by the Company with the expectation that it would be used in further sanitation-salvage jobs. Only very high risk trees (Risk 4) were marked for cutting, which resulted in a very light cut of less than 600 board feet per acre.

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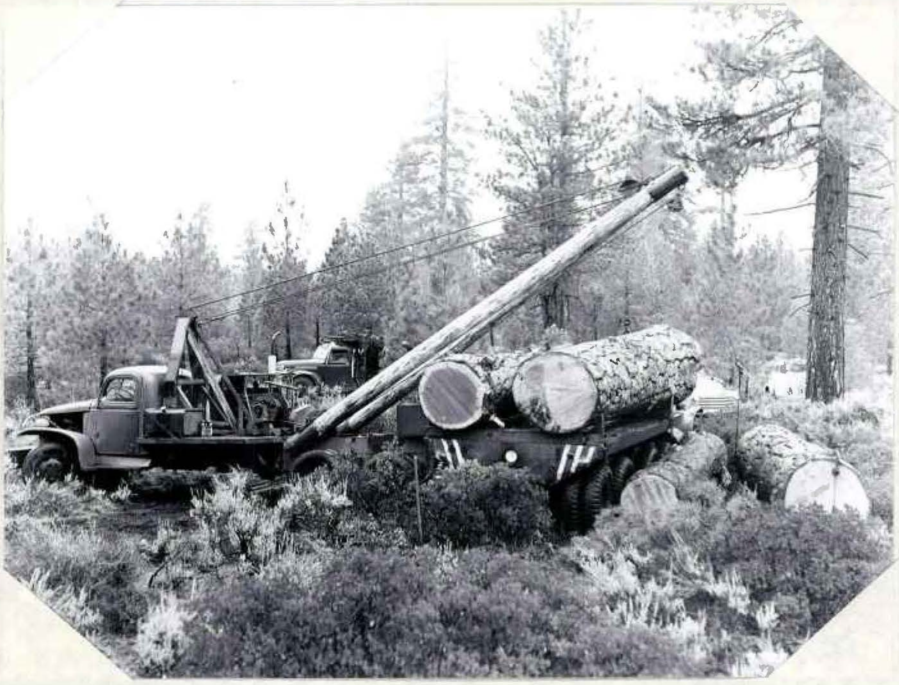

Figure 69.- Mobile log loader especially designed and used by Bill Hanan for salvage logging. Old Station, California, 1952.

BEPQ # 15665A

The Berkeley Forest Insect Laboratory cooperated with the Company in this experiment by indicating the type of trees to be cut and in studying the results as shown by sample plots. (U30) In a published article Bongberg (6) reviews the results of this test during 1939 and the five subsequent seasons:

Summary of Operations

1. Volume of risk trees salvaged (Risk 4 only) -	563 BF. per acre
2. Subsequent cumulative loss on treated area (1940-45)	81 BF. per acre
3. Subsequent cumulative loss on adjacent untreated areas	529 BF. per acre
4. Saving of stumpage resulting from operation	448 BF. per acre
5. Average annual reduction in loss	84.7%

It was figured that this 448 board feet per acre, which was saved for harvest at the end of the five-year protection period, more than offset the increased logging costs entailed by this light selective cut. The sanitation-salvage operation therefore paid for itself. If the direct cut-peel-burn method had been used, a cash outlay would have been necessary for the treatment of infested trees, very few of which could have been salvaged.

Rail Glade Area, Bly District, Klamath County, Oregon, 1940. Weyerhaeuser Timber Company.— In 1940, the Weyerhaeuser Timber Company initiated a test of sanitation-salvage in its extensive ponderosa pine holdings in southern Oregon, primarily to determine the advantage of substituting this method for that of direct control, which the company had been practicing for many years. The Rail Glade area of 960 acres located in the lower margin of the ponderosa pine type surrounding the Sprague River valley near Bly, Oregon, was selected for this first pilot operation. On this area an 18-year record of prior beetle-caused losses showed an average annual rate of 1.7 percent of the stand volume, and the prospect was that losses would continue to be high unless some action was taken to reduce them.

The Forest Insect Laboratory at Portland, Oregon assisted with the planning and tree selection, while Thomas J. Orr, Jr., Forester for the Weyerhaeuser Timber Company at Klamath Falls, directed the logging. The planning, initial phases, and results of the first two years were reported by Keen (U152, U157, U160). Bedard (U19) reported the third year's results and Bongberg reported the fourth and fifth years' (U32) and final results (U36).

The marking rule developed by Keen and Orr for this particular experiment integrated considerations of risk (current health), tree class, and value as follows:

Synopsis of Marking Rule

Risk Rating	Keen Tree Class	Value
Risk 4- Very high risk. All cut.	Cut all classes except age class 1	Cut all positive value trees. Cut negative value trees down to 12 inches if in groups and likely to contaminate valuable trees.
Risk 3- Sickly trees. Partly cut.	Cut susceptible classes in C and D and 4B trees if of declining vigor (-),except age class 1.	Cut some trees of normal vigor, in susceptible classes, if of high value.
Risk 2- Fairly healthy trees. None cut.	None cut even if of slightly declining vigor (-)	Not even high value trees in susceptible classes cut.
Risk 1- Healthy trees. None cut.	None cut.	Same as above.

In addition to the above, spike-top trees were cut if they showed signs of active insect work, otherwise they were left. Trees forking from a common stump were both taken if one was a risk tree.

Cull trees were cut from groups and dragged out into openings 50 feet away from the group so as not to cause attraction.

The cutting in 1940 covered 780 acres from which 895,380 board feet of high risk trees were removed. This represented a cut of 1,150 board feet per acre, which was approximately 18 percent of the total stand.

The final results were reported by Bongberg (U36). These showed yearly reductions in loss, as contrasted with the trend on untreated areas as follows:

1st year following treatment - 94.2% reduction
2nd year following treatment - 72.3" "
3rd year following treatment - 70.7" "
4th year following treatment - 73.4" "
5th year following treatment - 84.6" "
6th year following treatment - 88.2" "
Average, six-year period - 83.3" " 80.6

Summary of Operation

1. Volume of risk trees salvaged, 1940 1,150 B.F. per acre
2. Subsequent loss on treated area, 1940-1945 66 B.F. per acre
3. Expected loss if area had not been treated 396 B.F. per acre ?
4. Volume of timber saved on treated area 277 B.F. per acre
5. Average reduction in pine losses over period 83.3%

Bongberg concludes: "Final results of the experimental test of pine beetle control through sanitation-salvage logging proved to be highly satisfactory for a period of six years. All objectives of the test were met and the reserve stand was protected against excessive beetle-caused mortality until harvested during 1946."

Swede Cabin Area, Bly District, Oregon, 1941. Weyerhaeuser Timber Company.— The Swede Cabin operation was the second step in the development of a comprehensive sanitation-salvage program by the Weyerhaeuser Timber Company. Having found from the Rail Glade pilot test that this method only slightly increased the cost of log production, the Company made plans to expand this treatment to their extensive holdings in the eastside pine type. This expanded program was started in 1941 on a 6000 acre tract of the Sprague River drainage near Bly, Oregon, known as the Swede Cabin area.

That the Swede Cabin area contained a highly susceptible stand of ponderosa pine was evident from the fact that during the period 1930-1940 inclusive, bark beetles had killed 12.4 percent of the original stand estimated at 18,000 board feet per acre.

As reported by Bedard (U20), the rule for selecting trees to be cut on this area was essentially the same as that used on the Rail Glade area the previous year.

> "The exceptions were that negative value trees were not taken, badly leaning trees were taken, and the double root-crown principle was extended to include trees growing within 18 inches of each other. In addition, a special effort was made to thin groups and eliminate all possible high risk or so-called 'key trees' which might cause the entire group to be killed."

> "In training the marking crew, the Tree Class Slide Rule (72) and standard criteria for recognizing value were available to assist in securing uniformity in using these portions of the marking rule. In addition, a 'penalty system' of rating tree risk (13) was also devised by F.P. Keen to assist in training the markers to recognize poor risk and to differentiate between some of the characters. With no basic data available to show mortality ratios for the various crown characters, the penalties were estimated on the best judgement of Keen and the writer..."

This was the first area on which the penalty system of rating risk was put into operation.

Slightly over 3453 acres were logged during 1941 and 5,918 trees containing 5,621,200 board feet were removed. This was at the rate of about 1630 board feet per acre or 10.3 percent of the stand volume.

Results of the Swede Cabin operation were reported by Bongberg (U37). The benefits derived from this operation are shown on an annual basis in percent of loss reduction and board feet per acre in Figures and ,pages

Summary of Operation

1. Volume of risk trees salvaged 1,630 B.F. per acre
2. Subsequent loss on treated area,1941-47 incl. 110 B.F. per acre
3. Subsequent loss on untreated virgin area 387.7 " " "
4. Volume of timber saved on treated area 277.7 " " "
5. Average reduction in pine losses over period 71.5%

In respect to this operation Bongberg concluded: "The reduction in beetle-caused mortality which has been afforded by this cutting has been highly satisfactory for the seven years which have now elapsed since cutting."

These two sanitation-salvage operations were reported upon by Thomas J. Orr, Jr., Forester for the Weyerhaeuser Timber Company (96), who showed that the increased cost of logging on this light selection cut basis was between $1.50 and $2.25 per thousand feet; which should be offset by the value of the timber saved over a period of five or six years, if the salvage project is reasonably successful. He showed that "logs coming from a salvage operation will yield more No.2 Shop and better and more Box than the average log of the same stand, but less of the higher common grades. This yield is, of course, the characteristic of mature timber and the actual difference in dollar value is slight."

Following these trials, the Weyerhaeuser Timber Company adopted a partial cutting program on all of their holdings in Klamath and Lake Counties, Oregon (97). Selection of trees to be cut was defined in terms of Keen's age and vigor classes, to which were added the classes of current health developed by Salman and Bongberg (114). Determination of which trees in Keen's class 3 (mature) should be retained was based largely on the use of the tree class slide rule (72). The object of the marking was to leave in the reserve the high producing trees making the best growth. Up to 1945, more than 200 million board feet of timber was marked for cutting under this system. The results have been to leave a thrifty residual stand, in which losses have been negligible and the growth rate high.

Pringle Falls Experimental Forest, Oregon, 1950. Pacific Northwest Forest and Range Experiment Station, U.S. Forest Service.— Extending the concept of sanitation-salvage cutting into central Oregon's ponderosa pine forests, the Experiment Station carried out an additional trial of this method of beetle control on the Pringle Falls Experimental Forest near LaPine, Oregon, in 1950. The objectives of cutting, as stated by Sowder (115) were:

> "1. Remove live trees highly susceptible to insect attack and thereby reduce current and future insect losses.
>
> "2. Remove merchantable trees that are dead or dying from all causes and thereby salvage timber that would otherwise be lost.
>
> "3. Establish a permanent road system to facilitate future salvage or other cutting operations.
>
> "4. Reduce fire hazard and aid fire control."

A "penalty system" of rating risk devised by Bongberg in 1949 (115) in collaboration with T.J. Orr and C. Borsting of the Weyerhaeuser Timber Company was used as a basis for tree selection. Trees with a penalty score of 9 or more were considered as high risk and were marked for cutting.

The treatment was applied to 3,020 acres from which an average of 1.2 high risk ponderosa pine trees per acre with 1,606 board feet or 9 percent of the total pine volume were removed. Returns of $24.29 per M. bd.ft. were received and the total logging cost, including road construction, averaged $23.07 per M. bd.ft. Sowder estimated that this treatment will produce a net gain, due to growth, of $1.07 per acre per year over the next 10 years.

Inland Empire.— That the same principles of risk rating and sanitation-salvage cutting may be successfully applied to the ponderosa pine stands of the Inland Empire has been pointed out by Johnson (56). Cruises of mature ponderosa pine stands in the Kootenai River and Fisher River areas of Montana showed that the risk element ran between 12 and 17 percent of the stand volume, which was comparable to the 16 percent found at Black's Mountain in California. Actual sanitation-salvage cuttings have been carried out,but the results are not now available.

General results.-- All of the trials made of sanitation-salvage so far show it to be an effective measure for reducing mortality in east side ponderosa pine stands subject to attack by the western pine beetle and in Jeffrey pine stands attacked by the Jeffrey pine beetle; and for "beetle-proofing" these stands for periods up to 15 years. Reducing losses is a most effective measure for increasing net growth. The principle of removing high-risk beetle-susceptible ponderosa pines in the first cut has now been generally adopted through the interior ponderosa pine type of California, Oregon, Washington, and Idaho. (__1__).

There are, however, certain qualifications which should be recognized which limit the applicability of the method, i.e.

1. The highly favorable control results have been obtained only in the mature, slow-growing ponderosa pine stands of the eastside type. The adaptability of the method to the more thrifty westside pine stands is still in question and requires further study.

2. Sanitation-salvage does not apply to other portions of the ponderosa pine region, where such aggressive bark beetles as the Black Hills beetle or the mountain pine beetle are dominant. Nor does this method necessarily apply to other timber species and the control of other insect species. The applicability of sanitation-salvage as an insect control measure will have to be determined specifically for other insects and other hosts.

3. The period during which it has been under trial has been characterized by low endemic infestations, and it is yet to be proven that it will maintain control under the impact of aggressive, epidemic bark beetle infestations.

4. The use of sanitation-salvage is limited by a number of physical factors such as terrain, roads, and other transportation developments, and the availability of mill facilities for converting the susceptible trees into lumber.

Figure 70 .— A load of logs from a sanitation-salvage cutting being hauled out of the woods.

Differences between Areas in Results of Sanitation-Salvage

While all of the sanitation-salvage tests described in these recent reports show highly favorable control benefits over periods from one to ten years, there are noticeable differences between areas in the behavior of bark beetle infestations following cutting and in the degree of control effects that were achieved.

(Page 720a follows)

Figure 70 .-A load of logs from a sanitation-salvage cutting being hauled out of the woods.

BEPQ # 11111 I

A comparison of the Black's Mountain and Swede Cabin operations is shown in Figure 71 , on the basis of the percent of reduction in pine losses on the area cut by sanitation-salvage as compared with the loss on adjacent untreated areas. This comparison shows the relative effectiveness of two operations in preventing bark beetle losses. The Black's Mountain treatment was the most effective. It showed over 85 percent reduction in losses for the first seven years. After the seventh year it showed a gradual reduction in benefits through the tenth year. The Swede Cabin area showed a similar high degree of loss reduction for the first three years, then an erratic pattern of loss reduction through the seventh year, and then a rapid reduction in benefits through the tenth year. The reasons for these differences between areas is obscure. They may be due to differences in the rate of deterioration of mature pine stands, seasonal climatic conditions, the influence of surrounding beetle infestation, such as in windfalls, and other factors which act to modify the results of sanitation-salvage control.

Figure 71 .—Comparison of two projects in eastside pine type showing variable results in bark beetle control from logging high risktrees.

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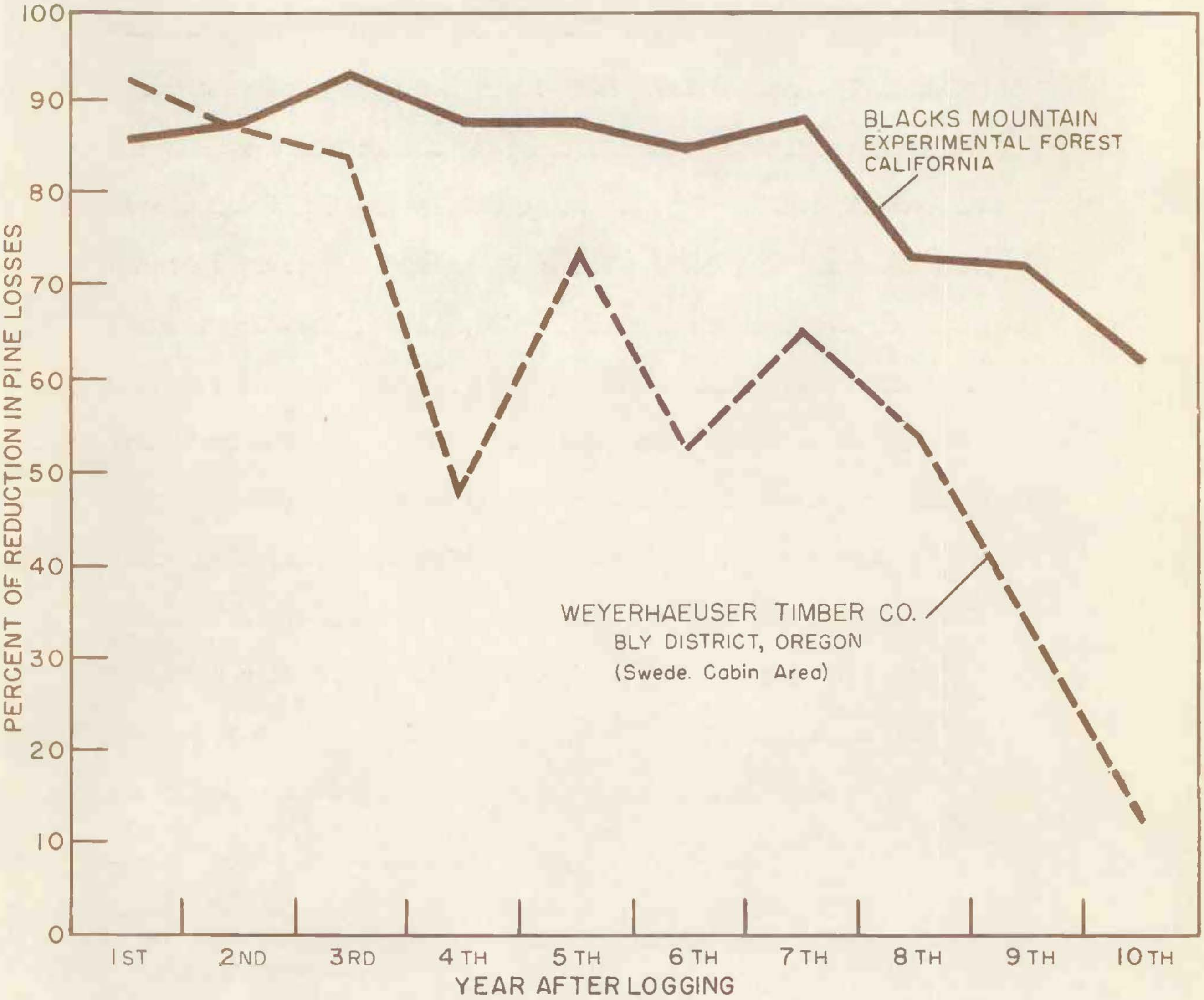

Figure 71.-- Comparison of two projects in eastside pine type showing variable results in bark beetle control from logging high risk trees.

Comparison of Benefits Obtained by Direct and Indirect Methods of Bark Beetle Control in the Burney Area, Shasta County, California.

Bark beetle control work in the Burney area during the winter of 1946 provided the first opportunity to compare the results of direct and indirect methods in the eastside ponderosa pine type under almost identical conditions of site, climatic factors, and the infestation cycle. The areas involved are included in the Burney Flat control unit of 27,700 acres located mostly north and east of the town of Burney, Shasta County.

A serious outbreak of _Ips_ _oregoni_ and _Ips_ _confusus_ occurred in this area during the summer of 1944, which was followed by an increasing western pine beetle infestation during the fall of that season. This situation was brought under control by the cut-peel-burn method during the late winter and spring of 1945 through a project organized by state, private, and federal timber owners. (U81). Following this initial control work, it was found in the fall of 1945 that an endemic infestation of the western pine beetle still persisted in most of the control unit. State and private owners felt that direct control should be continued on a maintenance basis to protect the results achieved by the initial control work. On the other hand, entomologists of the Forest Insect Laboratory recommended sanitation-salvage control because experience in previous projects had indicated that direct control could not have much effect in reducing an endemic infestation of the kind then existing in the Burney area. The program finally decided upon included the following phases:

1. Treat by direct peel-cut-burn western pine beetle infestation on areas which had been treated the previous year. This was intended primarily as a maintenance control program.

2. Initiate sanitation-salvage on areas which had not been given the benefit of any previous treatment.

3. Establish a protection zone around the Burney Falls State Park by sanitation-salvage of high risk trees, plus the cut-peel-burn treatment of infested unmerchantable trees, cull logs, butts, and tops. This treatment has been termed "modified sanitation-salvage."

The 1946 operation provided an excellent test of the effectiveness of the three different methods that were used. Consequently, the Forest Insect Laboratory at Berkeley set up a series of half section plots in the treated areas and measured the losses on these plots for the period 1946 to 1950 following the control work. Similar plots and loss studies were made in adjacent virgin stands where no control work was done. Results of these studies were summarized in reports by Bongberg (U33,U34). The following table shows the relative effectiveness of the different treatments.

	Acres sampled	Pine loss - board feet per acre		
		Before control	After control	
		1945	1946	1947
Virgin areas- no control	1,826	65.1	49.1	62.3
Cut-peel-burn (Maintenance control)	2,532	55.9	66.7	86.5
Sanitation-salvage	1,176	111.0	27.4	17.4
Modified sanitation-salvage	676	82.1	24.0	6.2

Figure 72 presents a comparison of results from these three methods of control in graph form. This shows that direct control, although it was applied over a large acreage, had little or no effect on this endemic infestation as subsequent losses even exceeded those in the virgin areas. On the other hand, sanitation-salvage was followed by an immediate reduction the first year and even greater reduction the second year. However, the additional benefits derived from the more intensive modified sanitation-salvage treatment are not considered to be enough to warrant the additional costs of this method.

Figure 72.—Comparison of results by direct and indirect methods of bark beetle control, Burney area, Shasta County, California, 1945 to 1947 inclusive.

Policy Statements Applying to Indirect Control

Economic considerations must largely dominate the recommendations for the use of indirect control methods such as sanitation-salvage. Transportation developments in the area, facilities for logging and milling the salvaged material, and available markets must first be taken into account as these factors largely determine whether or not indirect control is feasible. The statement published by Keen and Salman in 1942 (76) was the first applying to general policy in the applicaton of sanitation-salvage control.

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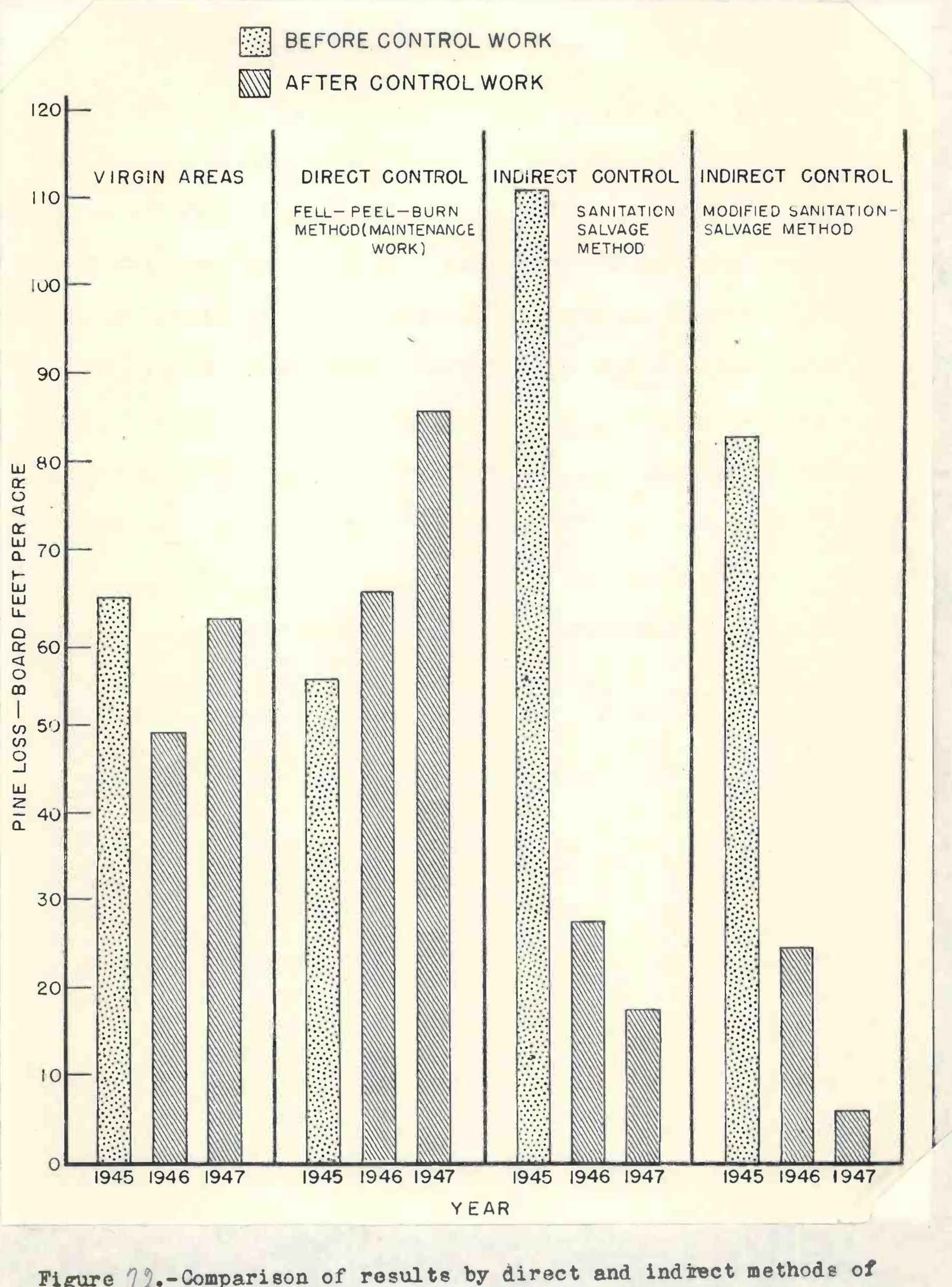

Figure 72.-Comparison of results by direct and indirect methods of bark beetle control, Burney Area, Shasta County, California, 1945 to 1947 inclusive.

> "Beetle control through tree selection and sanitation logging offers many advantages over the previous fell-peel-burn method of direct control. Results of tests so far show a greater reduction in subsequent losses than is usually obtained by the older method. However, the recovery of timber values which would otherwise be lost may offset the cost of treatment and may even yield a profit. On the other hand, this method is limited in its application to commercial timber stands of fairly high value and that can be reached by logging operations at a reasonable cost. This method is not appropriate for beetle control in parks, recreational areas, or inaccessible commercial forest areas in rough terrain. For such situations as these, fell-peel-burn or other direct control methods still offer the only practicable measures that can be used."

This policy statement was supplemented by Keen's restatement of bark beetle control policy of April 1, 1949 (U162):

> "In all western pine stands such silvicultural measures as thinnings and partial cuttings for improved forest sanitation, particularly the selective cutting of trees of poor thrift and the removal of "high-risk" trees, tend to leave a more vigorous residual stand of timber which should be more resistant to bark beetle attack. Therefore, such measures are endorsed as a part of sound timber-management practices and for whatever benefit may be gained in minimizing bark beetle losses.
>
> "For the present, sanitation-salvage logging as a bark beetle control measure will be recommended only for the virgin, commercial ponderosa pine and Jeffrey pine stands on the east slope of the Sierra Nevada and Cascade Mountains in California, Oregon, and Washington, where the percentage of "high-risk" trees (as defined by Salman and Bongberg (114) in the stand exceeds ten percent and where a light cutting is feasible from the economic standpoint - i.e., where the cost of the work can be largely offset by the value of logs salvaged. In high-hazard areas (Hazard V zones) and on fringe areas where the high-risk element of the stand exceeds 40 percent of the volume, some system of heavy cutting to utilize merchantable timber will normally be recommended, rather than a sanitation-salvage cutting for beetle control purposes only.
>
> "In westside stands of ponderosa, sugar, and Jeffrey pine and in all white pine and lodgepole pine stands, sanitation-salvage logging as a measure of bark beetle control is not being recommended at the present time."

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